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A Report on the Herpetofauna of the Vizcaíno Peninsula, Baja California, México, with a Discussion of its Biogeographic and Taxonomic Implications

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Abstract.—The Sierra Vizcaíno and Sierra Santa Clara are located along the west coast of central Baja California and compose the continental portion of the Vizcaíno Peninsula. A survey of the herpetofauna of this region documented the presence of several previously unreported species. Three species (*Gambelia wislizenii, Coleonyx variegatus,* and *Crotalus exsul*) show a close morphological similarity to conspecifics of Isla de Cedros. The presence of a relict mesophilic species, *Hyla regilla,* in the Sierra Vizcaíno, suggests that this region was much more mesic in the past. It is hypothesized that the saxicolous taxa of the Sierra Vizcaíno and Sierra Santa Clara colonized these mountains from the Peninsular Ranges of Baja California while the former existed as Pacific islands during the last 10,000 years. Such habitat specialists would be unable to disperse across the flat, sandy, Vizcaíno Desert that currently separates these species from their peninsular counterparts.

The Vizcaíno Peninsula is a prominent physiographic feature of the western coastline of central Baja California. It is composed of two mountain ranges, the Sierra Santa Clara and the Sierra Vizcaíno, and three offshore islands: Natividad, Cedros, and San Benitos (Fig. 1). Many areas of Baja California lack sufficient biological investigation but none more so than the Vizcaíno Peninsula. This is due largely to its isolation in the western portion of the Vizcaíno Desert and the associated difficulty in gaining access to it. Recently, access to these mountain ranges has been made easier by the grading of two major dirt roads, although travel within the mountains themselves is still largely restricted to foot or horseback.

Mosauer (1936) reported a few species of reptiles from the Vizcaíno Desert but made no remarks concerning species of the Vizcaíno Peninsula. Wiggins (1969) reported on a biological expedition into the Vizcaíno Desert in 1961 but, again, only the eastern periphery was visited and the Sierra Santa Clara and Sierra Vizcaíno remained unexplored. The herpetofauna along the eastern border of the Vizcaíno Desert has become well known (Grismer 1994), primarily because of the paving of Mexican Highway 1. However, there are still very few published

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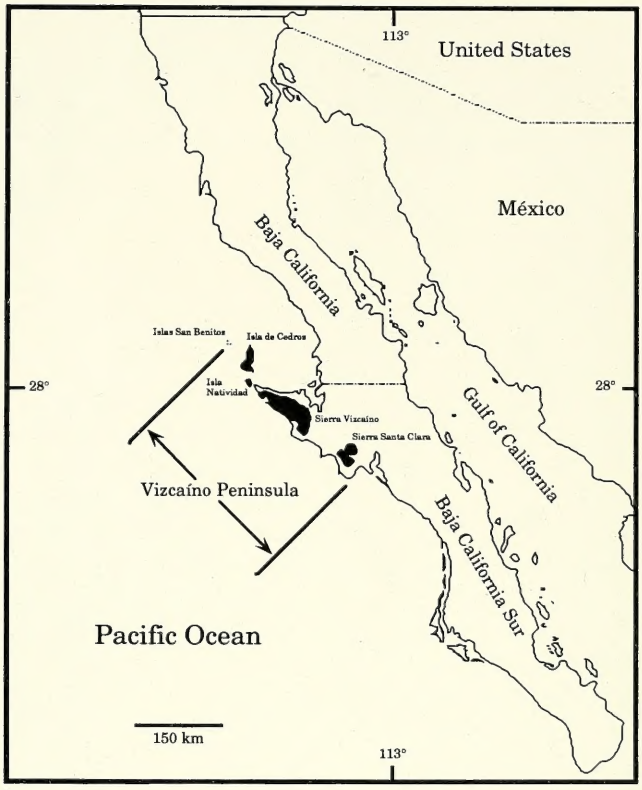

Fig. 1. Vizcaíno Peninsula of Baja California, México.

accounts of species from the western portion of the Vizcaíno Desert and virtually none from the continental portion of the Vizcaíno Peninsula. The intent of this paper is to document the distribution of the herpetofauna of the Vizcaíno Peninsula and discuss its historical, biogeographical, and taxonomic implications.

Materials and Methods

Study Area

The continental portion of the Vizcaíno Peninsula extends 204 km from Punta Abreojos in the southeast to Punta Eugenia in the northwest (Fig. 1). The Sierra Santa Clara, Sierra Vizcaíno, Isla Natividad, and Isla de Cedros existed as a large island or closely grouped archipelago of islands off the coast of western Mexico as early as 45 million years ago (mya) and remained insular until at least the late Pleistocene, 10,000 years ago (Gastil and Jensky 1973; Gastil et al. 1975). During the late Pleistocene, they formed a broad, land-positive connection with the rest of Baja California (Minch et al. 1976) because of lowered sea levels resulting from glaciation (Auffenberg and Milstead 1965). The subsequent rise in sea level to its current position fragmented the Vizcaíno Peninsula and resulted in the isolation of Islas Natividad and Cedros but left aerial connections between the Sierra Vizcaíno, Sierra Santa Clara, and the remainder of Baja California.

The dominant feature of the southeastern base of the Vizcaíno Peninsula is the Sierra Santa Clara (Fig. 2). This range consists of seven separate volcanic peaks

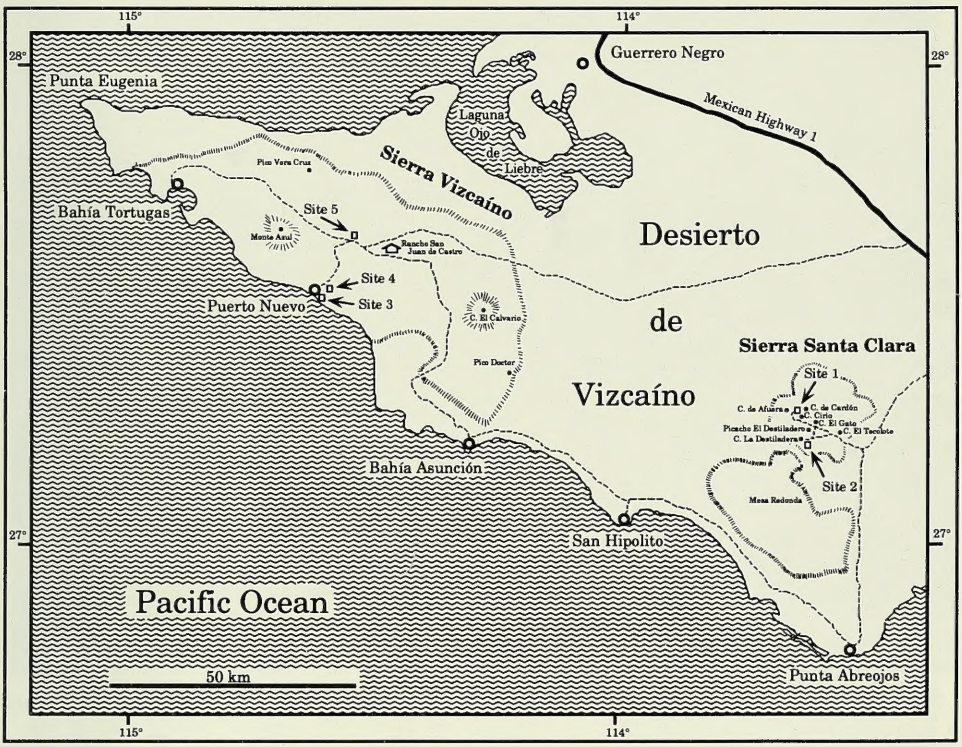

Fig. 2. Study area within the continental portion of the Vizcaíno Peninsula.

rising to between 600 and 1010 m in elevation above the flat, lowland, central portion of the Vizcaíno Desert. These mountains extend approximately 12 km northwest to southeast and are separated by one large and several smaller arroyos. North of the Sierra Santa Clara and south of the Sierra Vizcaíno lies the westernmost edge of the Vizcaíno Desert. As elsewhere, this portion of the Vizcaíno Desert is principally flat and featureless except for a few small volcanic mesas of low elevation, offering only a small degree of topographical relief (Fig. 3).

The Sierra Vizcaíno is a much larger mountain range than the Sierra Santa Clara and separated from it by approximately 50 km of open desert (Fig. 2). The Sierra Vizcaíno extends 115 km from Bahía Asunción in the southeast, tapering to Punta Eugenia in the northwest and reaches 900 m in elevation. Like the Sierra Santa Clara, the formation of the Sierra Vizcaíno is the result of Miocene volcanic deposition and the range has been aerial since the beginning of the formation of the Gulf of California (Gastil and Jensky 1973).

The Vizcaíno Peninsula extends northwestward from Punta Eugenia in the form of the islands Natividad, Cedros, and San Benitos. Islas Natividad and Cedros are landbridge islands that have had an aerial connection with one another and the Sierra Vizcaíno within the last 10,000 years (Milliman and Emery 1968; Wilcox 1980). Islas San Benitos, which is composed of three relatively small closely proximate islets, is of continental origin (Crouch 1979) and it is not known if it has ever been connected to Isla de Cedros.

The climate of the Vizcaíno Peninsula is strongly influenced by the cold California Current flowing southward along the west coast of North America. Asso-

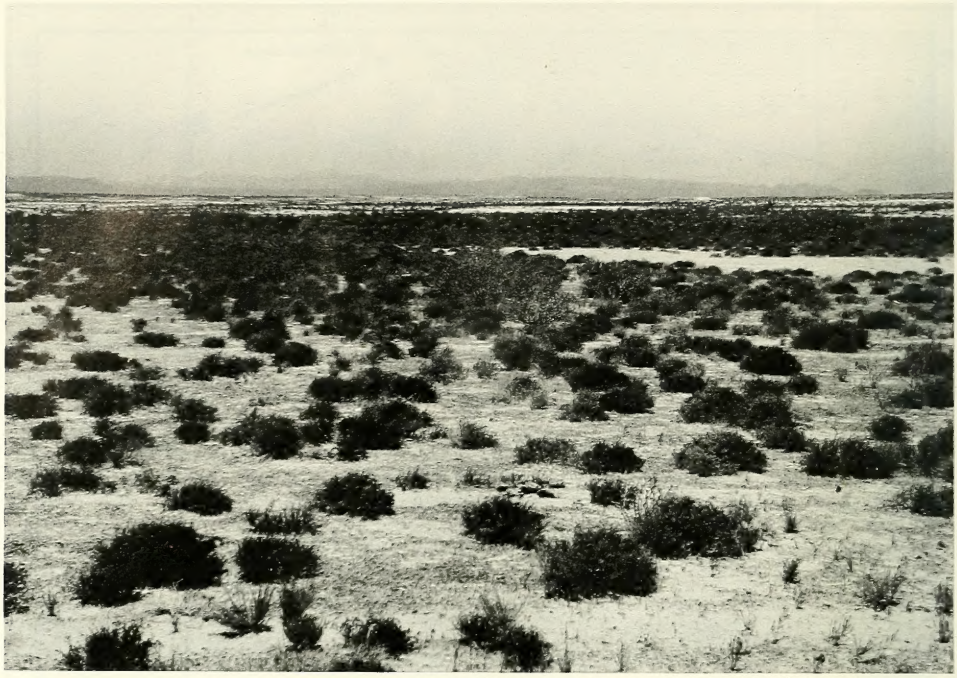

Fig. 3. Vizcaíno Desert between the Sierra Vizcaíno and the Sierra Santa Clara. Sierra Santa Clara in the background.

ciated with this cold-water current are cool, continuous onshore breezes which buffer the coastal areas of western Baja California from the considerably higher inland temperatures. Descending belts of warm, moist air at these latitudes contact the cold Pacific waters, causing fog to form which is blown inland by the onshore breezes. This creates a cool, humid climate which is reflected in an abundance of lichens and epiphytes that cover the rocks and vegetation along the coastal areas (Fig. 4). In fact, the west coast of central Baja California is one of only three fog deserts in the entire world (Meigs 1966). The Vizcaíno Peninsula lies at the southern extent of northern winter anticyclonic storm systems, and consequently, receives little in the way of winter precipitation, and even less from southern summer storms which come up from the Gulf of California or the eastern Pacific. Precipitation records from Bahía Tortugas and Punta Abreojos (Fig. 2) indicate annual amounts totaling 95 mm and 76 mm, respectively (Hastings and Humphrey 1969).

The Vizcaíno Peninsula lies within the Vizcaíno Desert, a biotic subprovince (Grismer 1994) of the Vizcaíno Region (Wiggins 1980). The Vizcaíno Desert is the most floristically depauperate and vegetationally scant area within the Vizcaíno Region, largely because of its low topographical relief and continuous winds. Generally, the dominant floral components are *Yucca valida, Fouquieria diguetii, Frankenia palmeri, Atriplex julacea,* and *A. polycarpa,* although floral diversity increases in many localized areas on hillsides and in valleys.

Observation Localities and Study Periods

The Sierra Santa Clara was visited by one of us (LLG) on 9–13 December 1988, by two of us (LLG and JAM) on 3–5 July 1990, and by all of us on 28 June to

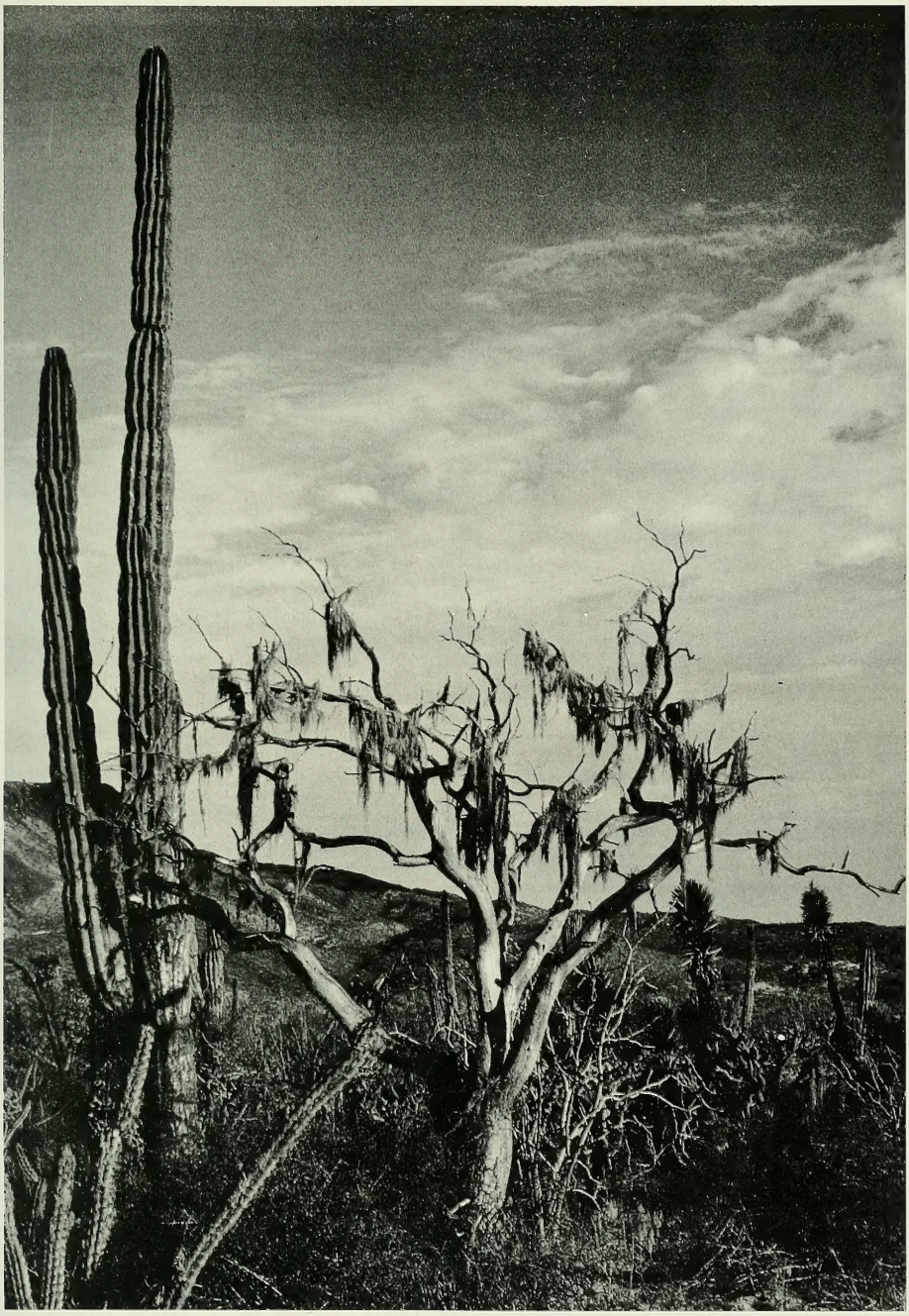

Fig. 4. Lichens on vegetation in the Sierra Santa Clara.

1 July 1991. Two principle study areas were used on all three visits. The first (site 1; Fig. 2) was near the abandoned Rancho Sierra Santa Clara in Arroyo Santa Clara between the rocky peaks of Cerro de Afuera and Cerro de Cardón (Fig. 5). This location allowed for the observation of saxicolous species on the hillsides and open-desert habitat generalists in the arroyo bottoms. The second study area

Fig. 5. Site 1 in Arroyo Santa Clara, Sierra Santa Clara.

Fig. 6. Site 2 at Rancho La Destiladera, Sierra Santa Clara.

(site 2; Fig. 2) was at Rancho La Destiladera at the base of the rocky and eroded Cerro La Destiladera (Fig. 6). Our observations at this site were biased towards saxicolous taxa. Observations were made both during the day and night at both study sites.

The Sierra Vizcaíno was visited by all of us on 1–3 July 1991. Three principle study areas were used which included a locale on the coastal bluffs (site 3; Fig. 2) at Puerto Nuevo (Fig. 7), and an inland locale approximately five km northeast of Puerto Nuevo (site 4; Fig. 2). The latter was situated within a small, sinuous, rocky arroyo emptying into Arroyo Puerto Nuevo and maintained small pools of semi-permanent water along its course (Fig. 8). An additional inland locality, approximately eight km northwest of the intersection of the roads to Bahía Tortugas and Puerto Nuevo (site 5; Fig. 2) was situated within a series of low, rocky foothills (Fig. 9). Observations at sites 4 and 5 were made both during the day and night. Observations were also made by two of us (LLG and JAM) throughout the southern portion of the Sierra Vizcaíno and southward along the coast to the Sierra Santa Clara.

Representatives of all species observed in both mountain ranges were photographed and released and voucher photographs deposited in the Los Angeles County Museum of Natural History (Appendix I). No animals were taken from the observation areas. Photographs were compared with preserved specimens (Appendix II) in an attempt to assess the degree of similarity of these specimens to those of surrounding regions, including Isla de Cedros.

Taxonomy

Recent debates in the herpetological literature have focused on the most appropriate application of species and subspecies concepts (Frost and Hillis 1990; Cole 1990; Echelle 1990; Highton 1990; Smith 1990; Collins 1991; Montanucci 1992; Van Devender et al. 1992; Lazell 1992; Grobman 1992; Collins 1992a, b; Frost et al. 1992; Grismer et al. 1994). We agree with Frost and Hillis (1990) and Frost et al. (1992) in that classifications should be lineage-based in order to reflect evolutionary history and it is our opinion that all taxonomic categories should attempt to represent demonstrably monophyletic lineages. Therefore, pattern classes and other paraphyletic assemblages should not be given formal taxonomic recognition. Unfortunately, the subspecies category usually is constructed to delimit the former (Smith 1990) and the herpetofauna of Baja California has been deeply entrenched in the practice of pattern class designation. This is not to say that pattern class designations are not useful in other ways, only that they are often inconsistent with lineage-based classifications. It is far beyond the scope of this paper to rectify this problem for the entire herpetofauna of Baja California, although such a work is currently in progress.

Because the Vizcaíno Desert is situated at a contact zone between two distinctive phytogeographic regions (the Vizcaíno Region to the north and the Magdalena Region to the south [Wiggins 1980]), many subspecies grade into one another at this latitude (Grismer 1994). Thus, we were forced to make taxonomic decisions based on our ability to identify particular subspecies. In the case of subspecies lacking contact zones at these latitudes, there was no problem with their identification and, thus, no taxonomic changes were proposed. However, for subspecies that did have contact zones in this region of the peninsula, it was sometimes

Fig. 7. Site 3 at Puerto Nuevo, Sierra Vizcaíno.

necessary to propose taxonomic rearrangements consistant with lineage concepts simply because the specimens in question could not be identified as one particular subspecies or another. Furthermore, the differences between such subspecies were non-discrete and clinal, indicating that they were continuously breeding pattern classes and not separate lineages. Unfortunately, much of this taxonomic rearrangement is concerned only with the peninsular subspecies of widely ranging continental forms simply because it was beyond the scope of this paper to consider insular and non-peninsular continental taxa, as well. In this respect, this work is incomplete; however, we do think that it is a step in the right direction.

Results

Two species of frogs, 10 species of lizards, 5 species of snakes, and one amphisbaenid were observed from the continental portion of the Vizcaíno Peninsula (Table 1). Those which represent significant new locality records and/or reveal some noteworthy characteristics concerning their geographic variation are discussed below.

Frogs

Bufo punctatus.—*Bufo punctatus* is widespread throughout most xeric regions of Baja California (Grismer 1994) but has never been reported from the Vizcaíno Peninsula. On 29 June 1990, two individuals were observed near site 1 in the Sierra Santa Clara. Both were above ground during the evening in the sandy arroyo bottom between Cerro Cardón and Cerro Cirio. Another individual was observed on 2 July 1991 at site 4 in the Sierra Vizcaíno near a shallow open well.

Fig. 8. Site 4 in the Sierra Vizcaíno.

Fig. 9. Site 5 in the Sierra Vizcaíno.

The Sierra Santa Clara toads had the typical red-spotted pattern observed in other *B. punctatus* from Baja California (Fig. 10a). However, the Sierra Vizcaíno individual was unique in that it generally lacked the characteristic large red spots encircled with black (Fig. 10b). Additional material from the Sierra Vizcaíno will be needed to further assess the significance of this pattern variation.

Hyla regilla.—Jameson et al. (1966) and Duellman (1970) reported that San Ignacio, Baja California Sur (BCS) was the northernmost locality of *H. regilla* in BCS. At approximately 1300 hrs on 2 July 1991, five transformed *H. regilla* and several tadpoles were observed in a shallow open well at site 4 in the Sierra Vizcaíno (Fig. 8). Approximately 100 m further up the arroyo, one additional frog (Fig. 11) and several tadpoles were observed in a small (ca. 2 m × 3 m) natural pool beneath some rocks. Approximately 0.25 km west, in this same arroyo, additional frogs were observed in moist vertical cracks in a shear rock face above a small pool. On 3 July 1991, another adult and several tadpoles were observed in a natural seepage in a shallow arroyo on the northwest side of Rancho San José de Castro, approximately 15 km southeast of the previous locality (Fig. 12). This arroyo had been greatly disturbed by cattle. We also heard one male calling. These localities represent a range extension of approximately 165 km to the west of San Ignacio and the first record of this species from the Vizcaíno Desert. Both localities had relict chaparral shrubs (*Rhus lentii* and *Malosma laurina*) near the water sources.

The color pattern variation observed in these specimens was extensive, ranging from solid dark or light brown to solid lime green with varying degrees of mottling. Duellman (1970) indicated that *Hyla regilla* from San Ignacio were *H. r. curta*

Table 1. Taxa of the continental portion of the Vizcaíno Peninsula. SV = known from the Sierra Vizcaíno; SSC = known from the Sierra Santa Clara; VD = known from the surrounding Vizcaíno Desert; and asterisked taxa are new records reported here for the first time. Reported but not confirmed taxa come from discussions with ranchers at Rancho San Ramón in the Sierra Santa Clara.

Confirmed	Distribution	Reported from SSC but not confirmed	Suspected but not reported
*Bufo punctatus**	SV, SSC	*Coleonyx switaki*	*Elgaria paucicarinata*
*Hyla regilla**	SV	*Chilomeniscus cinctus*	*Eumeces lagunensis*
Callisaurus draconoides crinitus	VD	*Lampropeltis getula*	*Sceloporus occidentalis*
*Cnemidophorus h. hyperythrus**	SV, SSC	*Leptotyphlops humilis*	*Arizona elegans*
*Cnemidophorus tigris**	SV, SSC	*Lichanura trivirgata*	*Crotalus mitchellii*
*Cloeonyx variegatus abbotti**	SV, SSC, VD	*Masticophis flagellum*	*Crotalus viridis*
*Dipsosaurus dorsalis**	SSC, VD	*Pituophis melanoleucus*	*Masticophis lateralis*
*Gambelia wislizenii copei**	SV, SSC, VD		*Phyllorhynchus decurtatus*
Phyrnosoma coronatum	SV, SSC, VD		*Sonora semiannulata*
*Sauromalus australis**	SV, SSC		*Tantilla planiceps*
Scleoporus magister rufidorsum	SV, SSC, VD		
Uta stansburiana	SV, SSC, VD		
*Crotalus enyo enyo**	SV, SSC		
*Crotalus exsul exsul**	SV, SSC		
*Hypsiglena torquata**	SSC		
*Salvadora hexalepis klauberi**	SSC, VD		
*Trimorphodon biscutatus lyrophanes**	SSC		
Bipes biporus	SSC, VD		

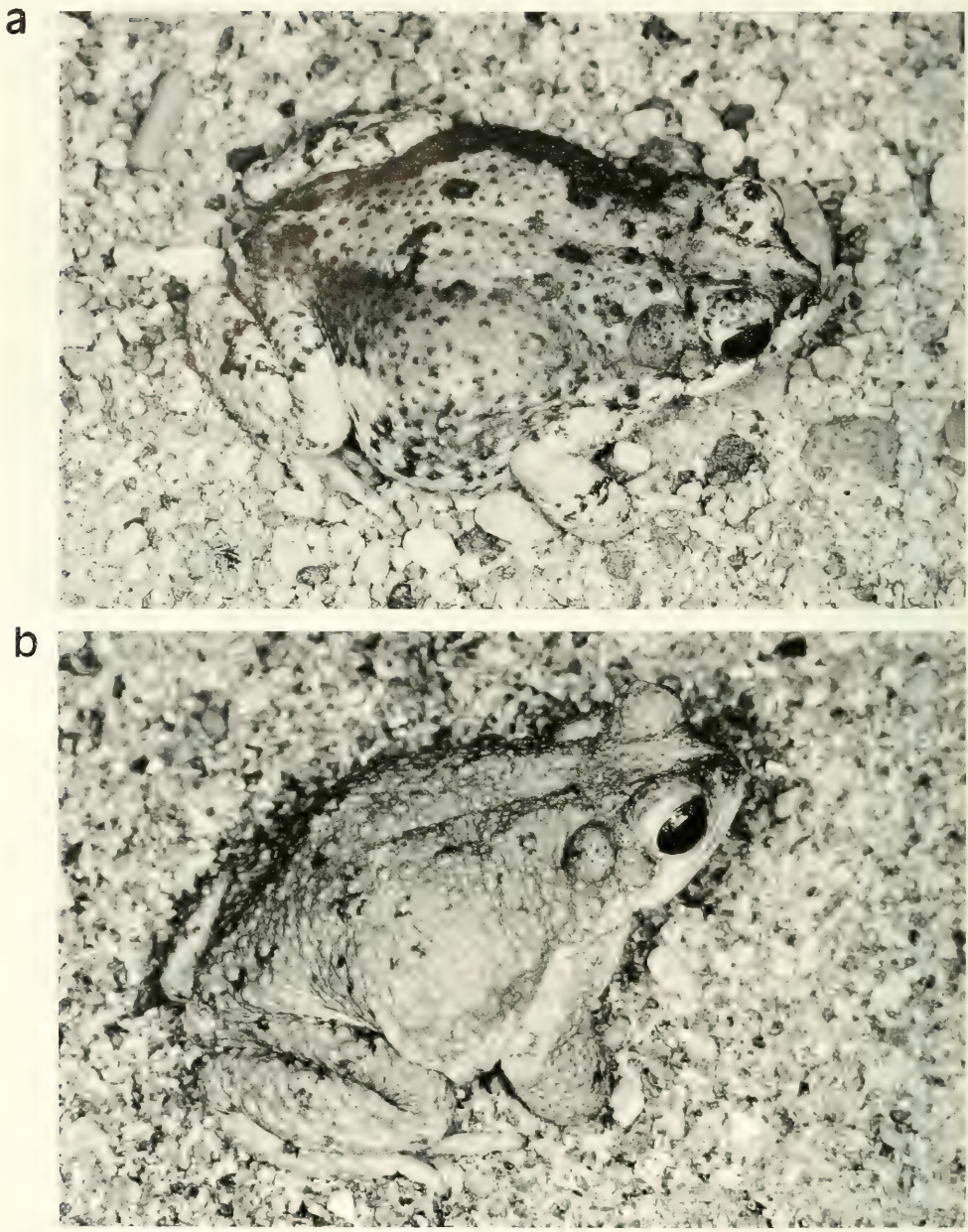

Fig. 10. a) *Bufo punctatus* from the Sierra Santa Clara. b) *B. punctatus* from the Sierra Vizcaíno.

and those from Isla de Cedros and northern Baja California were *H. r. hypochondriaca*. He separated these two subspecies on the basis of subtle differences in coloration, skin tuberculation, and hind limb length, all of which widely overlap. We found these characters variable in the Sierra Vizcaíno populations (limb length not examined) as well as in those from San Ignacio and Boca de la Sierra, BCS, and Isla de Cedros and Misión San Borja, Baja California (BC). Furthermore, a

Fig. 11. *Hyla regilla* from five km northwest of Puerto Nuevo, Sierra Vizcaíno.

Fig. 12. Habitat of *Hyla regilla* from Rancho San José de Castro, Sierra Vizcaíno.

review of the data presented by Jameson et al. (1966), indicates that similar variation exists among the remaining populations (subspecies) of *H. regilla.* Thus, we consider these to be pattern classes (*sensu* Frost et al. 1992) rather than diagnosable lineages and choose not to give them formal subspecific recognition.

Lizards

Gambelia wislizenii.—*Gambelia wislizenii copei* ranges along the entire length of Baja California (Banta and Tanner 1968). *Gambelia wislizenii neseotes* from Isla de Cedros was described by Banta and Tanner (1968) as a subspecies distinct from *G. w. copei* on the basis of differences in scalation, body proportions, and snout–vent and tail length. However, for both scale counts and body proportions, ranges overlapped widely and no attempt was made to demonstrate that the variation was statistically significant. Furthermore, they stated that a unique characteristic of the Isla de Cedros population was its large size. This phenomenon of alleged gigantism was compared to the condition seen in *Uta palmeri* of Isla San Pedro Mártir, *Crotalus mitchellii angelensis* from Isla Ángel de la Guarda, and *Sauromalus varius* of Isla San Esteban. However, in their table they compared average snout–vent lengths and included juvenile specimens among their samples. Furthermore, the largest specimen they examined was from the peninsula, not Isla de Cedros. For these reasons, Montanucci (1978) chose not to recognize *G. w. neseotes,* a decision with which we agree.

Nevertheless, specimens from Isla de Cedros have a distinctive dorsal pattern in comparison to specimens from the northern portion of the peninsula. Populations from the western foothills of the Sierra San Pedro Mártir and the rest of cismontane northwestern Baja California are typically chocolate brown in coloration with a pair of large, asymmetrically arranged paravertebral spots that are separated by broad cream-colored transverse bars (Fig. 13a). There is much lateral flecking, although lateral spots are absent. The large dorsal spots begin to break apart in more southern populations and lateral spots begin to appear. The deterioration of the dorsal spotting is most extreme in populations from the Vizcaíno Desert and Isla de Cedros. In these populations, only traces of the large paravertebral spots are visible (Fig. 13b). The break-up of the dorsal pattern appears to be ontogenetically regulated as all *Gambelia wislizenii* neonates have well defined paravertebral spots (Fig. 14a) and older juveniles from Isla de Cedros (SDSNH 7249) have been observed with dorsal patterns very similar to those seen in adult specimens from northwestern Baja California. The presumed ontogenetic deterioration of the dorsal pattern ultimately results in a pattern characterized by fine speckling and may be related to the extremely fine aeoleon substrate that predominates in the Vizcaíno Desert. However, this substrate does not predominate on Isla de Cedros and one of us (LLG) has observed an individual as high as 700 m in elevation on Isla de Cedros on coarse, dark, gravelly soil. Live leopard lizards in the vicinities of both the Sierra Vizcaíno (site 5) and the Sierra Santa Clara (site 2), and throughout the Vizcaíno Desert, have a dorsal ground color of light golden tan (Fig. 14b). Again, this may be associated with the substrate of the region. Montanucci (1978) discussed dorsal pattern polymorphism in *G. wislizenii* and hypothesized that the variability in dorsal patterns observed in this species are related to crypsis.

Dipsosaurus dorsalis.—*Dipsosaurus dorsalis* is known to range the entire length

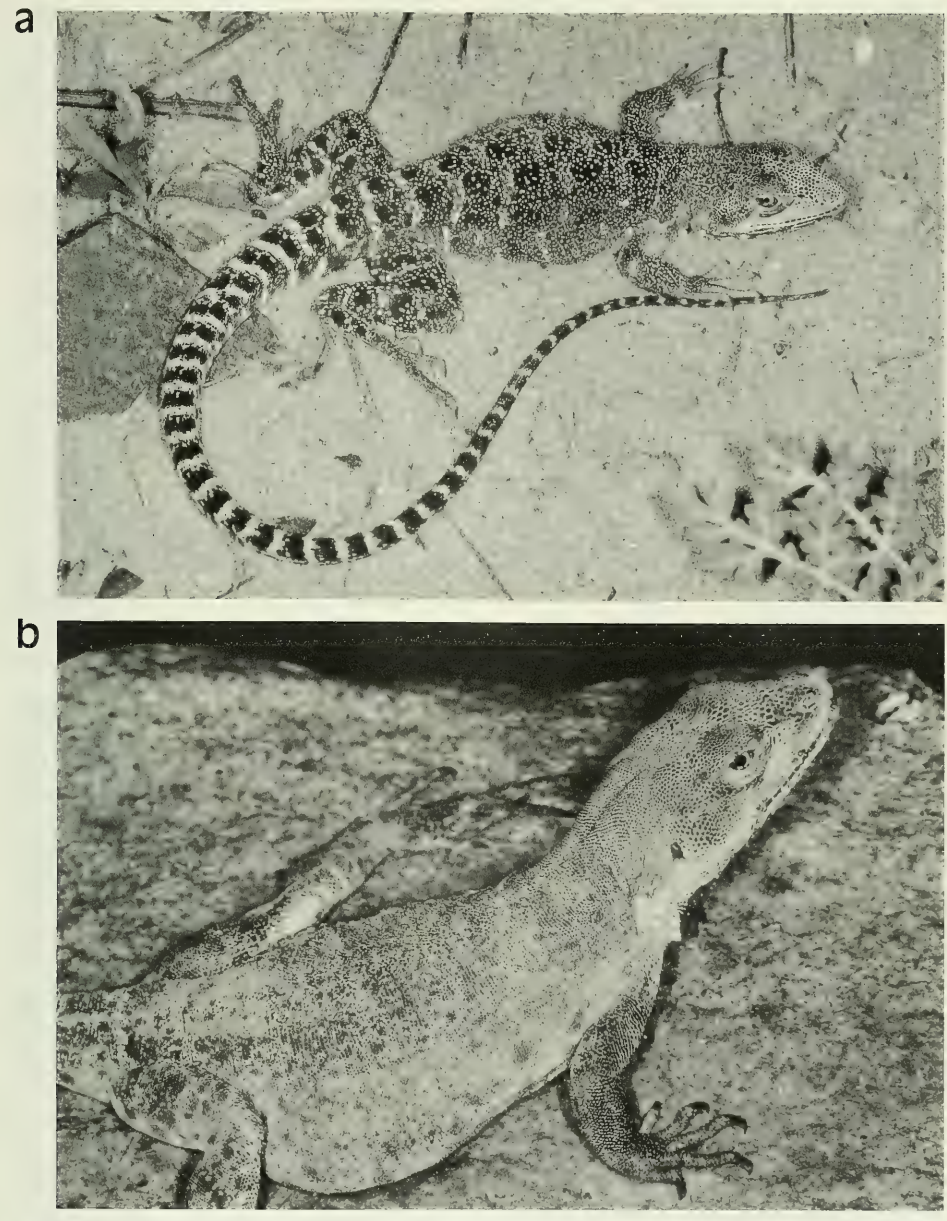

Fig. 13. a) Adult *Gambelia wizlizenii copei* from just north of Bahía de San Luis Gonzaga and b) adult *G. w. copei* from Isla de Cedros (photo by D. Spiteri).

of Baja California (Smith and Holland 1971), yet no specimens have been reported from the Vizcaíno Desert. Individuals observed on 29 June 1990 at site 1 in the Sierra Santa Clara had dark lateral body patterns of reticulated ocelli and gular streaks that seem to place them within the subspecies *D. d. lucasensis* of southern Baja California. This is in contrast to a lighter, more lineate lateral body pattern and only faint (or absence of) gular streaks that are diagnostic of *D. d. dorsalis* of

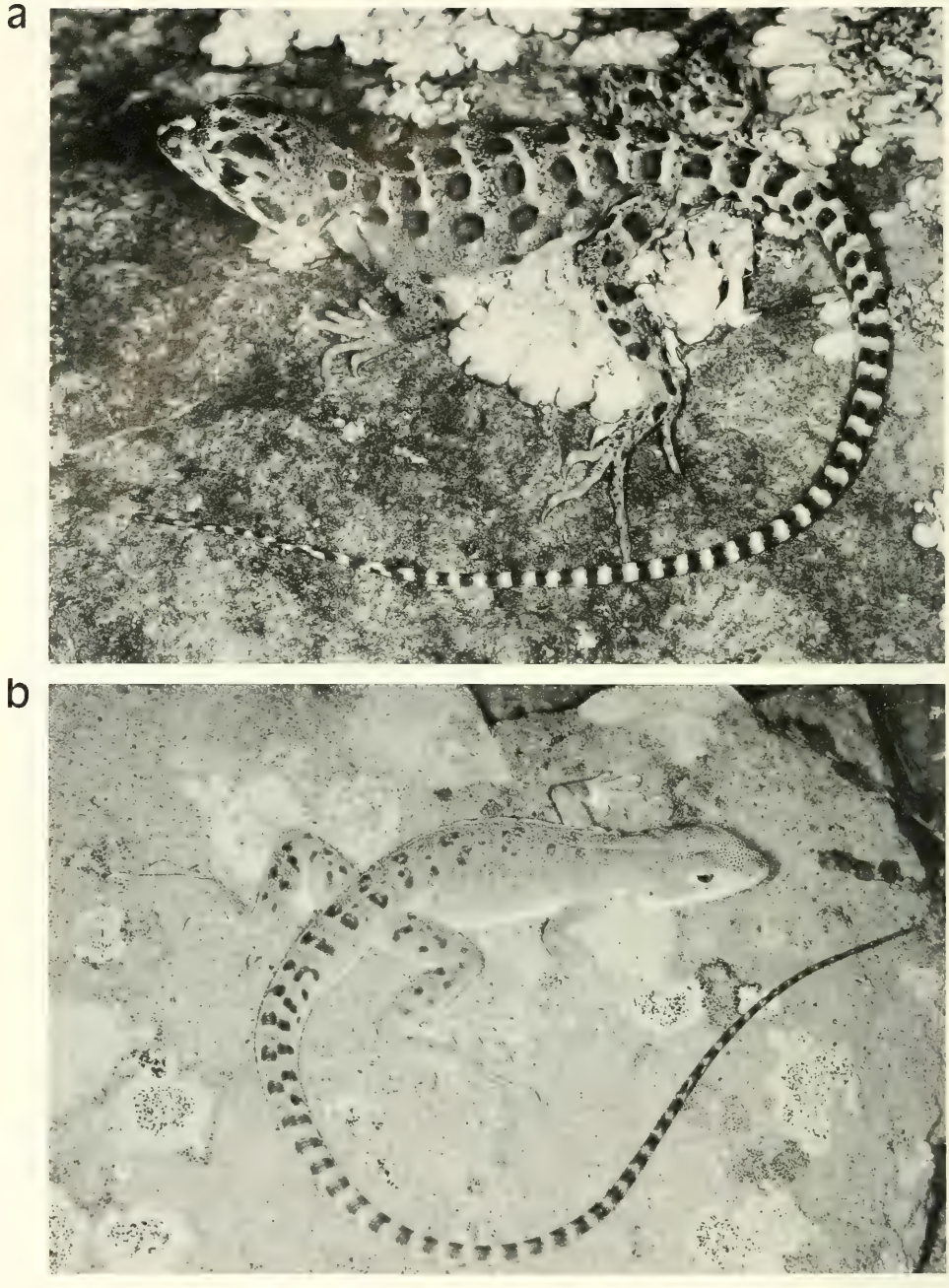

Fig. 14. a) Neonate *Gambelia wislizenii copei* from Isla de Cedros and b) adult *G. w. copei* from the Sierra Vizcaíno.

northern Baja California (Smith and Holland 1971). Smith and Holland (1971) noted a wide and subtle zone of intergradation in the number of rostral scale rows in the vicinity of San Ignacio between *D. d. dorsalis* and *D. d. lucasensis*. An examination of additional material from Baja California revealed that gular streaking in *D. dorsalis* is bold and prominent from San Ignacio southward into the Cape Region. However, such markings become lighter to the north, between San Ignacio and El Arco. At El Arco, approximately 65 km north of San Ignacio, gular streaking is prominent, but considerably lighter. At Bahía de los Ángeles, BC (approximately 100 km further north) and northward, gular streaking is faint to absent. Additionally, specimens from El Arco and southward generally have a dark-brown lateral body coloration with few if any longitudinal components. Much of the pattern is composed of large white dots encircled by dark-brown rings which, in some cases, encompass the entire interspace between the dots. This pattern is present to a lesser extent in some specimens from Bahía de los Ángeles, but generally body markings are lighter, and more longitudinally arranged. From Bahía de San Luis Gonzaga, BC (approximately 110 km further north) and northward, lateral body markings are reduced and faded (except in some cismontane populations in Valle de Trinidad) and have longitudinal markings. As would be expected in a continuously distributed species, lizards from the Sierra Santa Clara are intermediate in color pattern compared with those to the immediate north (El Arco) and south (San Ignacio).

These data demonstrate that the variation of each of these "diagnostic" characteristics is geographically discordant and broadly clinal, with postrostal scale row frequencies changing in the vicinity of San Ignacio, gular pattern changing in the vicinity of El Arco, and lateral body pattern changing between El Arco and Bahía de San Luis Gonzaga. Thus, we believe that these two subspecies are pattern classes and consider *D. d. lucasensis* (Van Denburgh 1920a) to be a junior synonym of *D. d. dorsalis* (Baird and Girard 1852).

Sauromalus australis.—*Sauromalus* is known to occur throughout Baja California (Gates 1968), with *S. australis* ranging from the approximate latitude of Bahía de los Ángeles southward to the northernmost portion of the Cape Region, BCS (Grismer 1994). Three individuals of *S. australis* were observed at site 1 and one at site 2 in the Sierra Santa Clara on 9 and 10 December 1988, respectively; three additional individuals were observed at site 5, and one more near site 4 in the Sierra Vizcaíno on 2 and 3 July 1991, respectively. These sightings in both the Sierra Vizcaíno and Sierra Santa Clara represent the first records of *S. australis* from the Vizcaíno Peninsula and range extensions of approximately 125 km southwest from Arroyo San Javier, BC (Bostic 1971) and 165 km northwest from San Ignacio, BCS. Comparison of color pattern revealed no substantial differences between chuckwallas of the Vizcaíno Peninsula and others from a comparable latitude in Baja California. Populations between Bahía de los Ángeles, BC and San José de Magdalena, BCS, have four to five dorsal transverse bands composed of small spots and reticulations, while the interspaces between these bands are finely spotted or speckled (Fig. 15). They also have a spotted or streaked gular pattern which sometimes extends onto the pectoral region. The color patterns of individuals from the Vizcaíno Peninsula were typical of other central Baja California populations, with the exception of two large adults from the Sierra Vizcaíno. These individuals had a reduced number of dorsal transverse bands; a prominent

Fig. 15. *Sauromalus australis* from San José de Magdalena, BCS.

second band, a less conspicuous third band, and the remaining portion of the dorsum finely spotted (Fig. 16a). The loss of bands is not uncommon for *S. australis* (Shaw 1945), although it is more typical of individuals from the southern portion of the peninsula.

Coleonyx variegatus.—Klauber's (1945) description of *C. v. abbotti* included those specimens ranging from cismontane southern California southward to near Rancho San José and Isla de Cedros, BC. Smith and Holland (1971) extended the peninsular distribution of this subspecies southward to Bahía de los Ángeles and Dixon (1970) extended it even further south to near the 28th parallel, although he presumed it to be absent from the Vizcaíno Desert. Curiously, Welsh (1988) considered a specimen (CAS 121182) from Bahía de los Ángeles to be an "apparently unreported northern range extension" for *C. v. peninsularis* of southern Baja California, despite the publications of Smith and Holland (1971) and Dixon (1970). One of us (LLG) has examined CAS 121182 and finds it to be typical of *C. v. abbotti* from this region.

Klauber (1945) noted that many specimens from Isla de Cedros have dark blotches within the light bands and the borders of the dark interspaces are irregular rather than straight (color pattern terminology following Grismer [1988a]). Klauber (1945) lacked material from adjacent peninsular localities with which to make comparisons. We find this same pattern present in *C. v. abbotti* from the Vizcaíno Peninsula. Several geckos matching Klauber's (1945) description of *C. v. abbotti* from Isla de Cedros were observed on 11 December 1988, 28–29 June 1990, and 3–4 July 1991 at both study sites within the Sierra Santa Clara. All had bands and interspaces of equal width with irregular borders and some had dark blotches within the interspaces. Two additional individuals were observed at site 5 in the

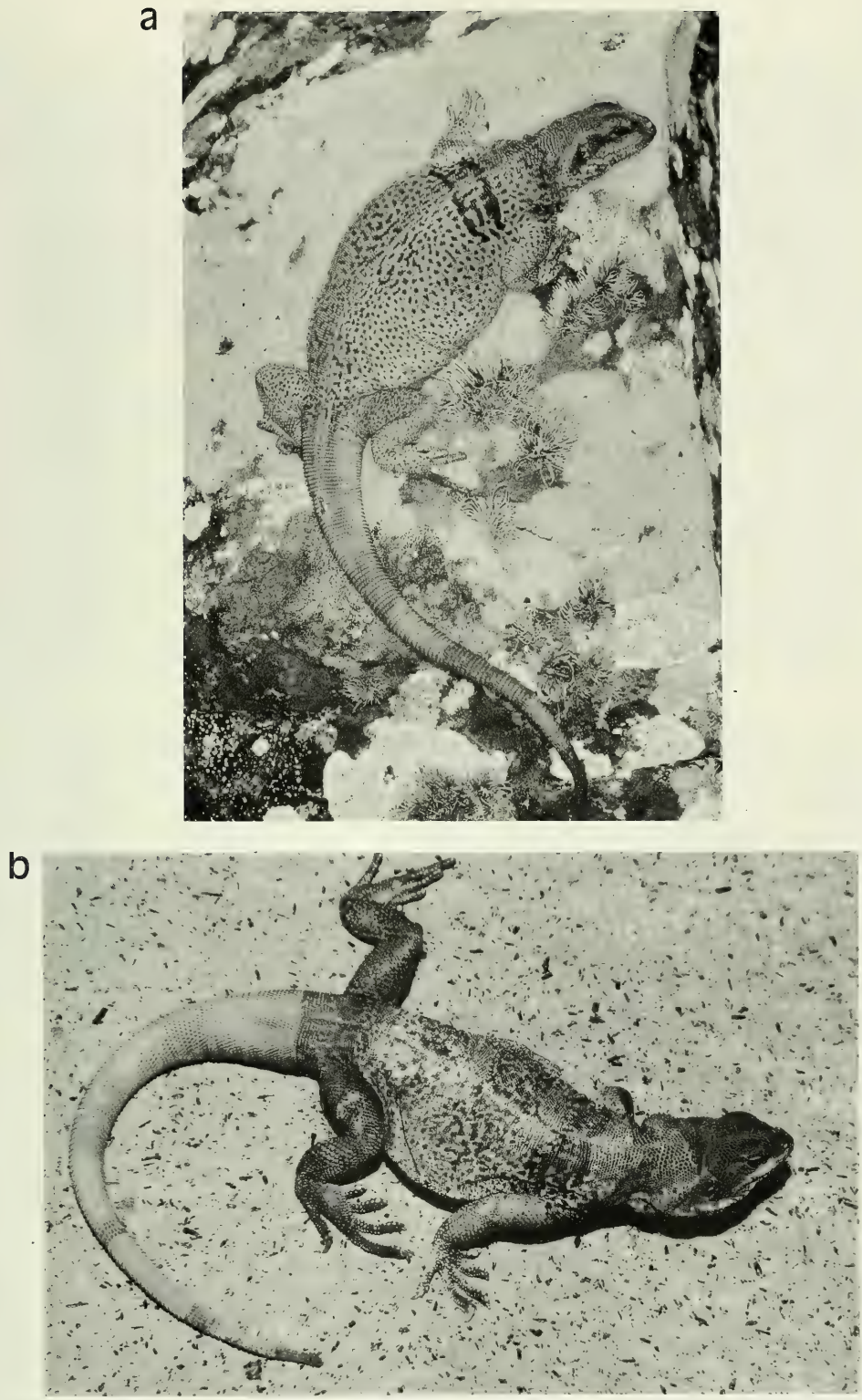

Fig. 16. a) *Sauromalus australis* from the Sierra Vizcaíno and b) *S. australis* from the Sierra Santa Clara.

Sierra Vizcaíno. Both specimens looked more typical of *C. v. abbotti* from Isla de Cedros than those from more northern peninsular localities. Both had bands and interspaces of equal width with prominent interspace blotching (Fig. 17). This pattern variation occurs in the southern populations of *C. v. abbotti.* It develops clinally and continues through the Vizcaíno Desert to the vicinity of San Ignacio. From here, it grades smoothly into the diagnostic pattern of *C. v. peninsularis* where the interspaces are narrower than the bands (Klauber 1945). This pattern continues from the vicinity of Mulegé, BCS southward. This demonstrates the pattern class nature of these diagnostic characteristics (Klauber 1945) and thus we think it more appropriate to consider *C. v. peninsularis* (Klauber 1945) a junior synonym of *C. v. abbotti* (Klauber 1945).

Cnemidophorus hyperythrus hyperythrus.—*Cnemidophorus h. hyperythrus* (*sensu* Welsh 1988) is known to range the length of Baja California, although it has never been reported from the Vizcaíno Desert. Several *C. h. hyperythrus* were observed foraging at the base of low vegetation at the foot of the mountains and along the banks of the arroyo at site 1 in the Sierra Santa Clara. Noticeably absent from within the Sierra Santa Clara, yet widespread in the surounding flats to the east of these mountains, was *C. labialis.* Apparently, these two small species of *Cnemidophorus* do not coexist within the Sierra Santa Clara. Several specimens of *C. h. hyperythrus* were also observed at site 5 in the Sierra Vizcaíno on 1–2 July 1991 and four specimens (CAS 147767–70) from 30 km north of Abreojos, BCS (Fig. 2) were examined. The nearest reported population of *C. h. hyperythrus* is from San Ignacio, approximtely 165 km to the east (Grismer 1994). The Vizcaíno Peninsula populations may represent a disjunct population within the Vizcaíno Desert. This hypothesis is supported by the fact that these two species range within 15 km of each other along the northwestern edge of the Vizcaíno Desert, but are not found sympatrically. One specimen of *C. labialis* (CAS 143163) was examined from six km east of Jesús María within the Vizcaíno Desert and two specimens of *C. h. hyperythrus* (CAS 90504-05) were examined from one km southeast of Rancho Mezquital in an ecotonal area between the Vizcaíno Desert and the more rocky inland areas of the Vizcaíno Region (*sensu* Wiggins 1980). Thus, habitat preference appears to be the limiting factor of these two species' distributions in central Baja California, with *C. h. hyperythrus* favoring more rocky and vegetated substrates and *C. labialis* more sandy habitats.

Cnemidophorus tigris.—Several large individuals of *C. tigris* were observed during the day foraging in the flats and arroyo bottoms on 28–30 June 1990 throughout the Sierra Santa Clara. This species also was observed at site 3 in the Sierra Vizcaíno on 1 July 1991 and in the open desert area between the Sierra Vizcaíno and Sierra Santa Clara. None, however, were observed in any inland areas within the Sierra Vizcaíno nor have any been reported. According to Smith (1946), the subspecies in this area is *C. t. stejnegeri* (*sensu* Grismer 1994). However, lizards observed at site 1 in the Sierra Santa Clara lacked the well-defined striping pattern of *C. t. stejnegeri* common in the more northerly populations from Baja California. The dorsal pattern of the Sierra Santa Clara individuals tended to be more mottled with a transverse orientation to their dorsal striping, similar to the much larger and adjacent eastern race, *C. t. rubidus* (Burt 1931). Schmidt (1922) also commented on the close resemblance in color pattern of specimens from this area to *C. t. rubidus* from further east, but believed them to

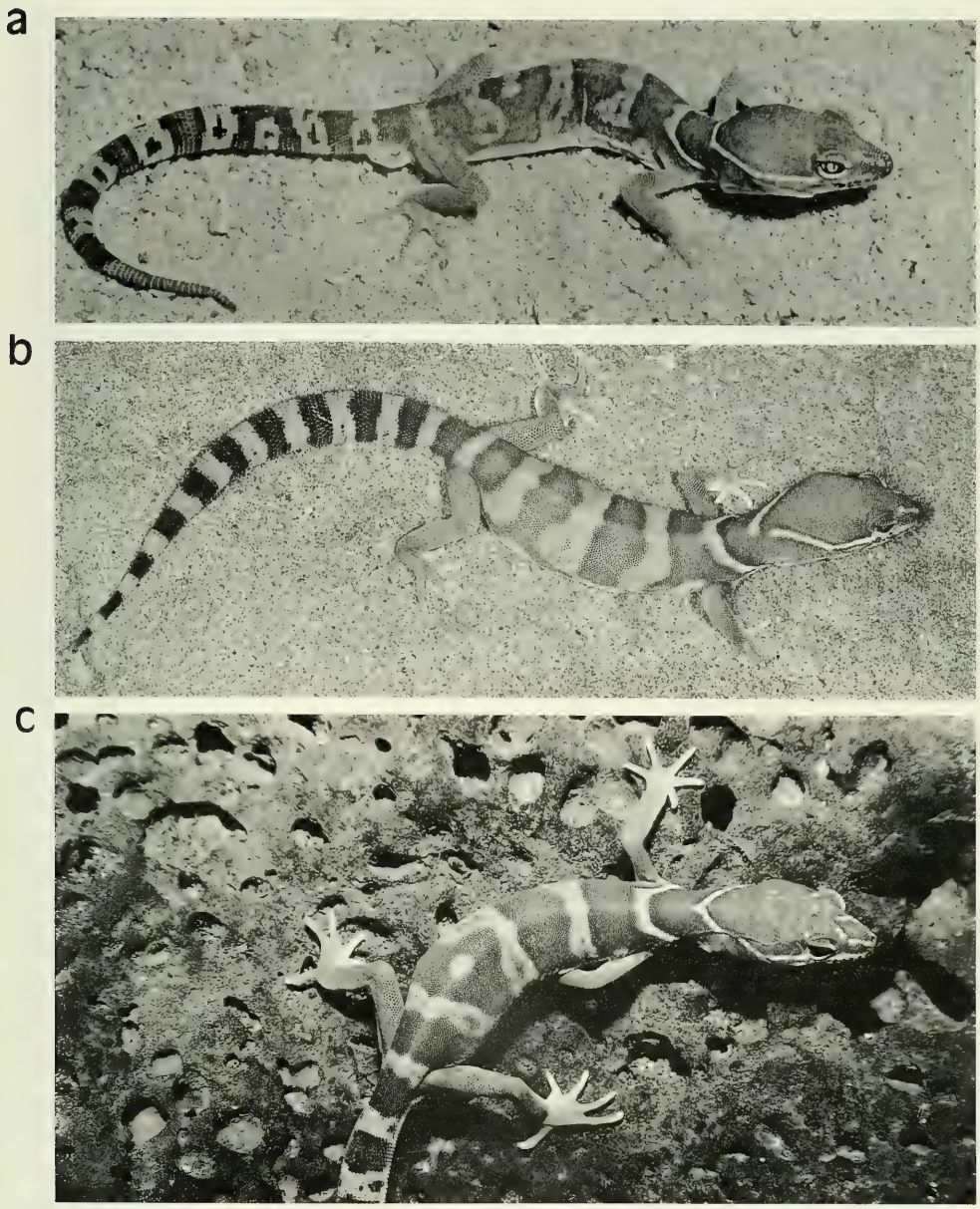

Fig. 17. a) *Coleonyx variegatus abbotti* from Isla de Cedros (photo by J. Tashjian), b) *C. v. abbotti* from the Sierra Vizcaíno, and c) *C. v. abbotti* from San Ignacio, BCS.

be derived from *C. t. stejnegeri*. Dickerson (1919) provided the name *C. bartolomas* for populations between Bahía Tortugas and Punta Abreojos (Schmidt 1922).

There are three general adult dorsal body pattern classes of *Cnemidophorus tigris* in Baja California. Those populations from the Lower Colorado Valley Region (*C. t. tigris*) have a faded dorsal pattern with fairly distinctive transverse com-

ponents, especially laterally. In populations west of the Lower Colorado Valley Region (*C. t. stejnegeri*), the dorsal pattern is boldly lineate. These two patterns blend smoothly into one another in low mountain passes (such as Paseo de San Matías, north of San Felipe) and at the southern end of the Lower Colorado Valley Region in the vicinity of Bahía de los Ángeles. From here southward, the third pattern class (*C. t. rubidus-maximus*) begins to develop a reticulated pattern overlaying the lineate pattern. Proceeding southward, the reticulations gradually increase and begin to dominate the dorsal pattern until ultimately the lineations are nearly obliterated in adult *C. t. maximus* from the Cape Region. A comparison of specimens from Bahía Tortugas and photographs of the Sierra Santa Clara specimens reveals that these two populations do not differ in dorsal pattern and both fall within this latitudinal cline. Thus, it appears to us, as it did to Schmidt (1922), that the Vizcaíno Peninsula populations are intermediate between "*C. t. stejnegeri*" and "*C. t. rubidus.*"

We would be inclined to do away with the subspecific names of the peninsular populations of *Cnemidophorus tigris* if it were not for the striking differences in hatchling and juvenile color pattern of *C. t. maximus* and *C. t. rubidus* of southern Baja California (yellow sinuous stripes and bright-orange to pink tails) and *C. t. tigris* and *C. t. stejnegeri* north of San Ignacio (straight white stripes and bright-blue tails). Until the degree of geographic contact and intergradation (if any) in these characters can be evaluated, we believe it is best to follow the current classification. If there is no geographic intermediacy in these characters, these forms may be different species. Unfortunately, tail coloration is only recognizable in living material.

Snakes

Hypsiglena torquata.—Hypsiglena torquata is considered to range widely throughout Baja California (Tanner 1944, 1966), including the Vizcaíno Desert, although no specimens have actually been reported from within the Vizcaíno Desert (Grismer 1994). Two individuals were observed on the evening of 29 June 1990 and another on 4 July 1991 at site 1 in the Sierra Santa Clara. None of these could be identified as any of the existing peninsular subspecies of Baja California. Two were unique among *Hypsiglena* (W. W. Tanner, pers. comm. 1991) in having an extremely faded and reduced dorsal body pattern and a thin dagger-shaped nuchal blotch (Fig. 18). The other was more typical in coloration and pattern. These represent both the first records of this species from the Vizcaíno Desert and a range extension to the west of approximately 165 km from San Ignacio. We believe that this is a disjunct population and that its absence from the Vizcaíno Desert is not an artifact of collecting because no specimens are known from the eastern periphery of the Vizcaíno Desert along Mexican Highway 1 (Grismer 1994).

The four peninsular subspecies of *Hypsiglena torquata* in Baja California all intergrade widely (Tanner 1944; Grismer 1994) and lack distinctive, discrete, diagnostic characteristics. Thus, we believe these subspecies represent pattern classes and choose only to recognize one form in Baja California, *H. t. ochrorhyncha* (Cope 1860a). It is likely that due to similar variation and intergradation in the other continental forms, the subspecies *H. t. nuchalata, H. t. chlorophaea,*

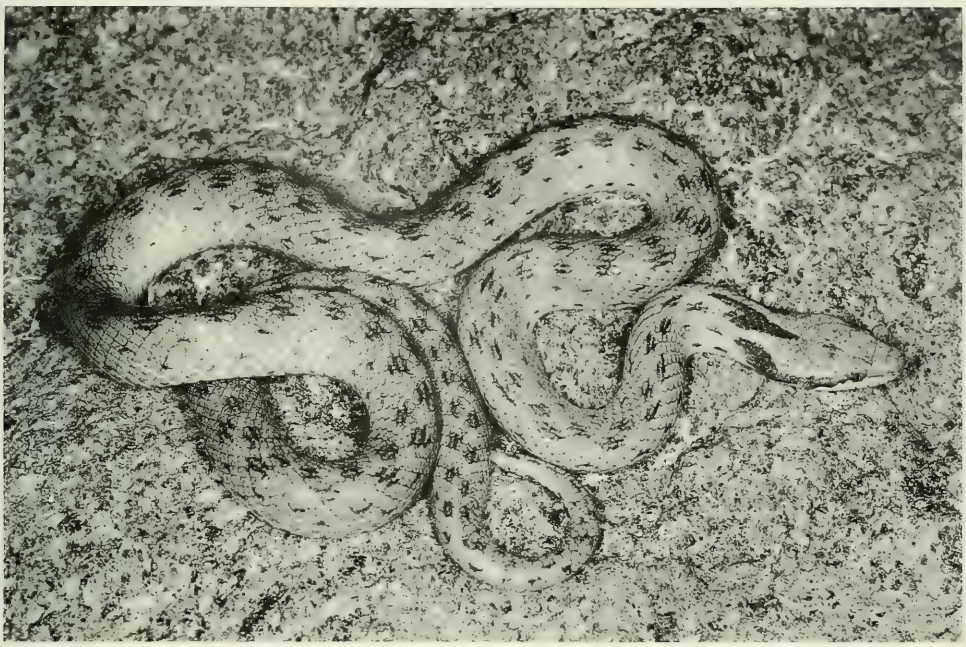

Fig. 18. *Hypsiglena torquata* from the Sierra Santa Clara.

and *H. t. texana* (Tanner 1944, 1985), should be reevaluated. This, however, will require additional investigation.

Salvadora hexalepis.—*Salvadora h. klauberi* ranges throughout the southern two-thirds of Baja California but has never been reported from the Vizcaíno Peninsula (Bogert 1945). One large adult was observed on the morning of 22 June 1990 as it was exiting a burrow at site 1 in the Sierra Santa Clara. Another was observed five km north of Punta Abreojos on 3 July 1991. Both appeared to be typical of all other populations of *S. h. klauberi* and represent the westernmost records for this species in central Baja California and the first records of this species from the Vizcaíno Peninsula (Bogert 1945).

Trimorphodon biscutatus.—*Trimorphodon biscutatus* ranges throughout Baja California but has never been reported from the Vizcaíno Peninsula (Scott and McDairmid 1984). One individual (Fig. 19), from an arroyo between Cerro Cirio and Cerro Cardón at site 1 in the Sierra Santa Clara, was observed. The subspecific status of this snake could not be ascertained due to variation in the "diagnostic" characters used to define the two subspecies currently recognized on the Baja California peninsula (Gehlbach 1971). The two subspecies, *T. b. vandenburghi* from the northern part of the peninsula and *T. b. lyrophanes* from the southern portion, possess no unique characteristics, and are differentiated from each other largely on the basis of a divided (*T. b. lyrophanes*) or undivided (*T. b. vandenburghi*) anal plate (Klauber 1940; Gelbach 1971). However, variation in this feature in both subspecies limits the utility of this character state in identifying individual specimens. Klauber (1940) found that 38 of 39 specimens of *T. b. lyrophanes* possessed a divided anal plate, although his concept of *lyrophanes* differed from that of the current taxonomy due to his inclusion of populations

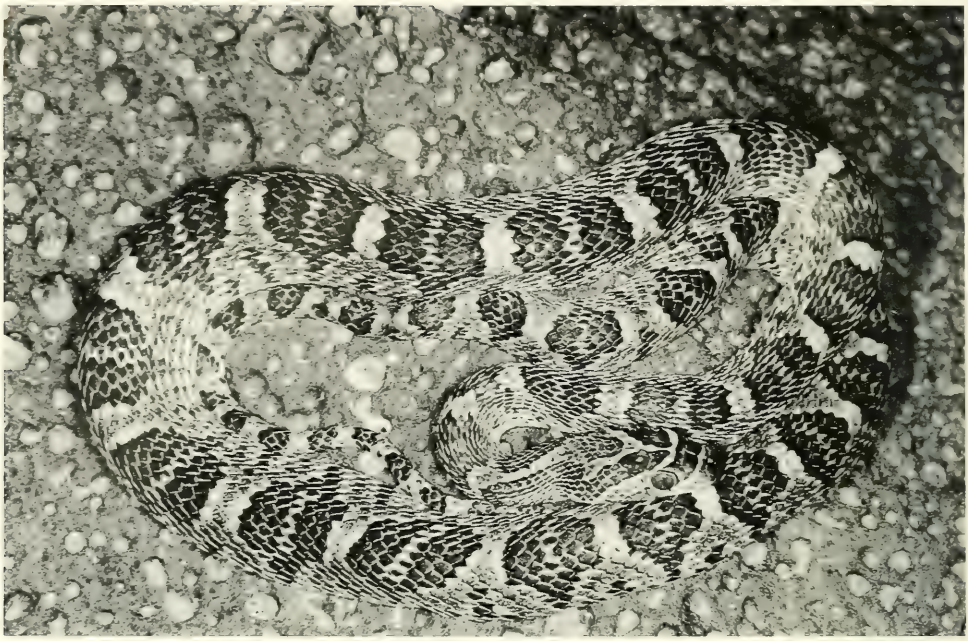

Fig. 19. *Trimorphodon biscutatus lyrophanes* from the Sierra Santa Clara.

from southeastern California, Arizona, Nevada, and western Utah. This was in contrast to his finding that *T. b. vandenburghi* possessed an undivided plate in 46 of 49 specimens. Klauber (1940) and all subsequent authors have considered this the single most important difference between these two subspecies. Additional statistically significant differences cited included a lower number of dorsal body blotches and greater numbers of supralabials, infralabials, and subcaudals in *T. b. lyrophanes.* However, the ranges for these scale counts overlap greatly and thus could not be used to identify the Sierra Santa Clara specimen.

The Sierra Santa Clara specimen possessed an undivided anal plate, the diagnostic character of *Trimorphodon b. vandenburghi.* The distributions of the two taxa have been proposed by Klauber (1940), Gehlbach (1971), and Scott and McDiarmid (1984). Klauber (1940) and Gehlbach (1971) considered all populations south of San Ignacio, BCS to be *T. b. lyrophanes* and all populations north of El Rosario, BCN to be *T. b. vandenburghi.* Scott and McDiarmid (1984), however, consider all specimens south of the vicinity of El Rosario (according to their distribution map) to be *T. b. lyrophanes.* This presumably was based on the examination of additional material between San Ignacio and El Rosario. The individual from the Sierra Santa Clara locality falls within the distribution of *T. b. lyrophanes* as reported by Scott and McDiarmid (1984), but its undivided anal plate suggests that it may be *T. b. vandenburghi.*

Clearly, suitable characters have not been discovered that allow the reliable diagnosis of individual specimens to a particular subspecies. In addition, the recognition of these two taxonomically distinct forms was first proposed when specimens were unknown between San Ignacio and San Diego County, California, leaving the possibilty that they were allopatric. We now know that this species is

continuously distributed in Baja California and that the "diagnostic" characteristics of the two subspecies are variable or overlap broadly. For these reasons we see no justification for recognizing two distinct forms of *Trimorphodon biscutatus* in Baja California and propose that *T. b. vandenburghi* (Klauber 1928) be considered a junior synonym of *T. b. lyrophanes* (Cope 1860b).

Crotalus enyo.—*Crotalus enyo* ranges from approximately Cabo Colonet, BC southward into the Cape Region, BCS (Beaman and Grismer 1994) but has never been reported from the Vizcaíno Desert. One specimen of *C. e. enyo* was observed during the day on 12 December 1988 and another during the night of 3 July 1991 from site 2 in the Sierra Santa Clara. Both were somewhat faded in overall coloration (Fig. 20b), which is surprising because most west coast populations are very dark (Lowe and Norris 1954). Two additional specimens were observed from site 3 on 1 July 1991 in the Sierra Vizcaíno. Both were dark colored (Fig. 20a), unlike those of the Sierra Santa Clara. These are the first records of this species from the Vizcaíno Desert and represent range extensions to the west from San Ignacio of approximately 165 km.

Crotalus ruber.—One indivdual of *C. ruber* was observed in the Sierra Santa Clara during the evening of 29 June 1990 at site 1 and another on 30 June 1990 at site 2 (Fig. 21a). An additional individual was observed in the Sierra Vizcaíno on the evening of 2 July 1991 at site 5 (Fig. 21b). Prior to these records, specimens from the Vizcaíno Peninsula were known only from Bahía Tortugas (Van Denburgh and Slevin 1921).

As it is currently constituted, *Crotalus ruber* ranges from southern California throughout all of Baja California, and *C. exsul* is restricted to Isla de Cedros (Klauber 1972). Previously, Van Denburgh and Slevin (1921), Schmidt (1922), and Van Denburgh (1922) considered the populations of central and northern Baja California, Isla de Cedros, and southern California to be *C. exsul.* Those of southern Baja California were considered to be *C. lucasensis* (Van Denburgh 1922) or *C. atrox lucasensis* (Schmidt 1922). Subsequently, Klauber (1930) restricted *C. exsul* to Isla de Cedros, and later recognized all peninsular populations as *C. ruber* (Klauber 1949). More recently, Brattstrom (1964) and Campbell and Lamar (1989) commented on the weak and inconsistent character differentiation between *C. ruber* and *C. exsul* and both suggested the two were possibly conspecific. This classification was subsequently followed by Minton (1992). We provide further evidence, based on the observations of the specimens listed above, that *C. exsul* and *C. ruber* lack consistent diagnostic characteristics.

These two species traditionally have been separated on the basis of putative differences in dorsal pattern, caudal bands, and head scale morphology (Gloyd 1940; Klauber 1972; Campbell and Lamar 1989). The dorsal pattern of *Crotalus exsul* consists of subcircular to nearly hexagonal anterior dorsal blotches which become more transversely elongate caudally. The dorsal blotches are uniformly colored without distinctive dark margins and lighter centers. The posterior borders of the anterior blotches are bordered with inconspicuous lightly colored scales. The dorsal pattern of *C. ruber* consists of rhombic or diamond-shaped dorsal blotches with the anteriormost blotches distinctly highlighted posteriorly. The dorsal blotches are usually uniformly pigmented, although they become outlined with dark brown or black in the southern portion of the range (Campbell and Lamar 1989). An examination of 24 *C. ruber* and 18 *C. exsul* (Appendix I) revealed

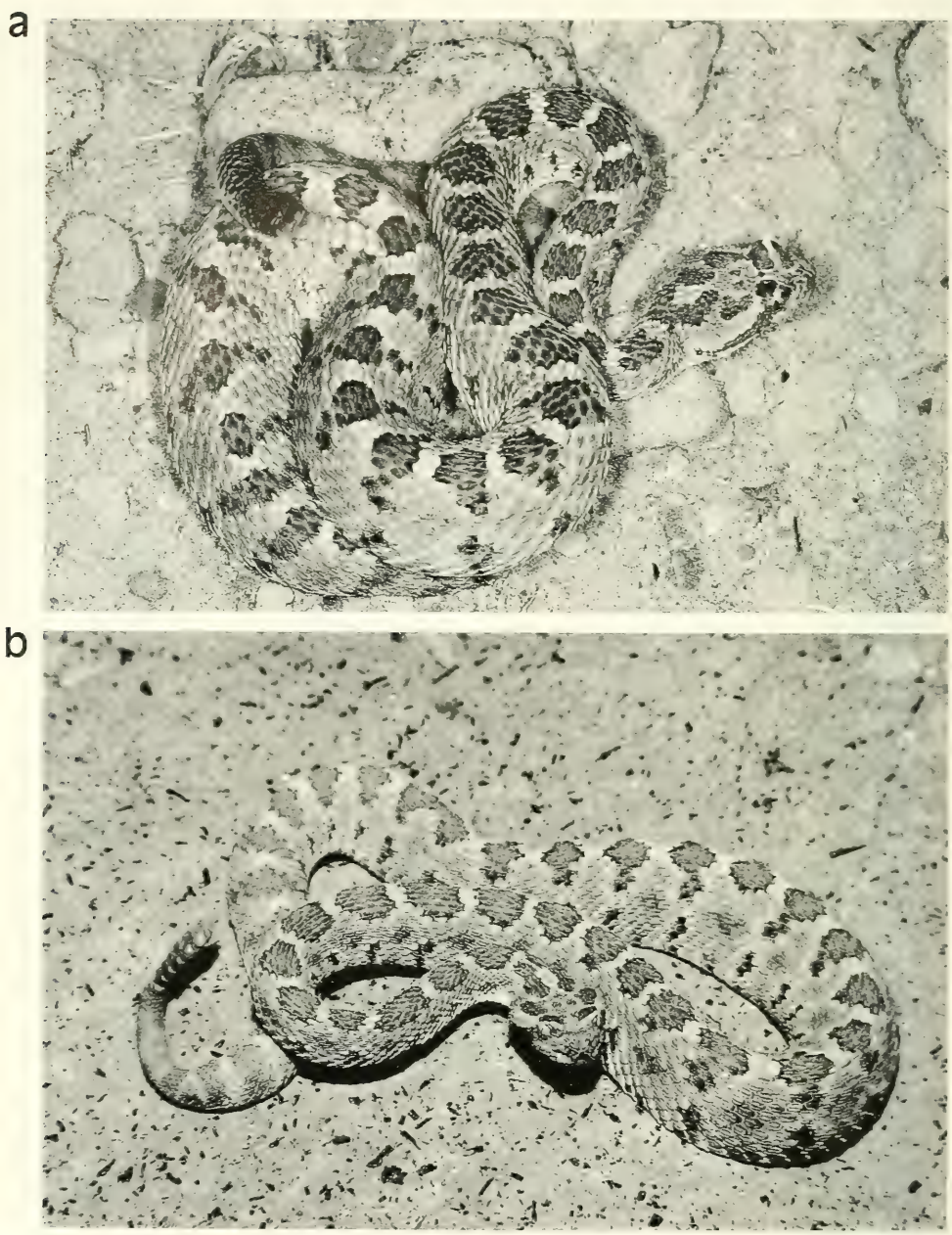

Fig. 20. a) *Crotalus enyo* from the Sierra Vizcaíno and b) *C. enyo* from the Sierra Santa Clara.

that 89% of *C. exsul* had poorly defined highlighting around their anterior dorsal blotches, whereas all *C. ruber* had anterior dorsal blotches with well defined highlighting. The individuals from the Sierra Santa Clara and the Sierra Vizcaíno had dorsal patterns intermediate between *C. ruber* and *C. exsul.* The dorsal pattern was also obscured anteriorly, with inconspicuous highlighting restricted to the posterior margins of the subcircular dorsal blotches (Fig. 21), which is the con-

dition more typical of *C. exsul.* However, the dorsal blotches tended to have dark borders with light centers, more typical of *C. ruber* from southern Baja California. The specimens examined from Bahía Tortugas (CAS 19826, 55886-87) had poorly defined dorsal patterns and were virtually identical to the majority of *C. exsul.*

In addition to the dorsal pattern variation, *Crotalus exsul* was distinguished from *C. ruber* by the presence in most specimens of laterally broken caudal bands, intergenial scales (interchinshields), and prenasals which do not make contact with the supralabials (Gloyd 1940; Klauber 1972; Campbell and Lamar 1989). In the material examined, laterally broken caudal bands occured in 94% of *C. exsul* and in 10% of *C. ruber.* The individual *C. ruber* from the Sierra Vizcaíno and one of the two from the Sierra Santa Clara had broken lateral caudal bands similar to *C. exsul.* Unfortunately, we are unable to comment on the scale characteristics of the individuals observed in the Sierra Santa Clara and Sierra Vizcaíno because these features are not visible from photographs.

Based on the above evidence, we believe as do others, that it is more consistent with the data at hand to consider *Crotalus ruber* (Cope 1892) a junior synonym of *C. exsul* (Garmen 1883). The variation seen along the Vizcaíno Peninsula may actually be clinal with the Sierra Vizcaíno and Sierra Santa Clara specimens being intermediate between those of Isla de Cedros and the Peninsular Ranges of central Baja California. Such a cline could have arisen along a longitudinal gradient during the land positive connection between Isla de Cedros and the continental portion of the Vizcaíno Peninsula.

In addition, the dorsal pattern and scale characters differentiating the peninsular subspecies *Crotalus exsul lucasensis* and *C. exsul exsul* are clinal in nature, intergrading in the vicinity of Loreto (Klauber 1949). We regard these two taxa as pattern classes and propose that *C. exsul lucasensis* (Van Denburgh 1920b) be considered a junior synonym of *C. exsul exsul* (Garmen 1883). It is beyond the scope of this analysis to consider the taxonomic validity of the insular subspecies *C. e. lorenzoensis,* which will require further investigation.

Discussion

Three of the species observed (*Gambelia wizlizenii copei, Coleonyx variegatus abbotti,* and *Crotalus exsul exsul*) from the Sierra Vizcaíno show a closer resemblance in color pattern to conspecifics of Isla de Cedros than to adjacent peninsular populations. This serves to underscore the historical geographical relationship between the continental and insular portions of the Vizcaíno Peninsula.

The presence of *Hyla regilla* in small relict populations from the Sierra Vizcaíno and Isla de Cedros (Grismer and Mellink 1994) indicates that at one time, the Vizcaíno Peninsula was much more mesic than it is today. Also supporting this hypothesis are the relict populations of chaparral shrubs found in association with the *H. regilla* populations. Unfortunately, there exists no paleontological evidence from the Vizcaíno Peninsula to address this hypothesis; however, evidence from other areas throughout Baja California strongly indicates that a much cooler and more mesic climate existed in this area. Baja California experienced little in the way of geologic change during the Pleistocene but along with the rest of North America, was affected by at least four southern expansions of the Laurentide Continental Glacier, which significantly altered the habitat and climate (Everenden and Everenden 1970). At low elevations, the interglacial periods were

Fig. 21. a) *Crotalus exsul* from the Sierra Santa Clara and b) *C. exsul* from the Sierra Vizcaíno.

considered xeric and there was a trend toward increasing aridity and the spread of desert habitats. These successive habitats proceeded from subhumid, semiarid, subdesert, to desert habitats (Axelrod 1966, 1975, 1979) with each successive interglacial. Based on mammalian fossil evidence from near San Miguel de Comondú (Miller 1977), central Baja California appears to have maintained a wood-

ed and grassland habitat with a relatively thick vegetative cover (Axelrod 1979). This is consistent with the findings of Wells (1969), showing that the region northwest of Cataviña in north central Baja California was covered with a juniper woodland during the Late Pleistocene, and Van Devender (1990), who demonstrated that Cataviña supported a mixture of juniper and chaparral plants during the early Holocene. Following the last glacial period the Wisconsin, 11,000 years ago, decreased winter rainfall caused the rate of this drying trend to rapidly increase, and desert habitats to spread throughout Baja California, culminating in the current more arid condition (Van Devender and Spaulding 1979). This rapid spread of deserts left several relict mesic refugia, along with their associated herpetofaunas, throughout Baja California (Grismer 1988b, 1990, 1993, 1994; Grismer and McGuire 1993; Grismer and Mellink 1994; McGuire 1989; McGuire and Grismer 1993). Therefore, there is still a strong possibility that additional relict mesophilic taxa such as *Sceloporus occidentalis, Eumeces skiltonianus* or *E. lagunensis, Elgaria paucicarinata, Masticophis lateralis,* and *Crotalus viridis* may still occur in the Sierra Vizcaíno. *Elgaria paucicarinata* and *Masticophis lateralis* both occur north and south of the Vizcaíno Peninsula in isolated populations (Grismer 1988b, 1990, 1993). *Crotalus viridis* ranges as far south as 16 km south of El Arco in the Vizcaíno Desert (Smith et al. 1971). *Eumeces lagunensis* is known from isolated mesic refugia of BCS as far north as Santa Agueda (Grismer 1994), and *S. occidentalis* was recently discovered in the higher elevations of Isla de Cedros in association with relict chaparral communities (Grismer and Mellink 1994).

The saxicolous species *Sauromalus australis, Hypsiglena torquata,* and *Trimorphodon biscutatus* probably colonized the Vizcaíno Peninsula from the Peninsular Ranges while the former existed as an archipelago of islands off the west coast of central Baja California. None of these species would be likely to disperse across over 100 km of aeolean sand to reach these areas from the nearest Peninsular Range source, and none have yet been reported from the Vizcaíno Desert. The Vizcaíno Desert probably has been inundated by the Pacific Ocean several times in the past (G. Gastil, pers. comm. 1990), the latest being within the last 10,000 years (Milliman and Emery 1968). At this time, passive overwater dispersal was the likely mode of transport of these taxa to the Vizcaíno Peninsula. Suprisingly, however, *Phyllodactylus xanti* is absent from this region. This species is a well-known overwater disperser as evidenced by the large number of islands (many of which are oceanic) on which it occurs in the Gulf of California (Grismer 1994) and it occurs along the cool west coast of Baja California north of the 28th parallel (Bostic 1971). Its absence from the Vizcaíno Peninsula remains unaccounted for.

Saxicolous species that have not been reported from the Vizcaíno Peninsula, but which occur at the same latitude in the Peninsular Ranges, are *Coleonyx switaki, Crotaphytus vestigium* (*sensu* McGuire, in prep.), *Petrosaurus thalassinus, Phyllodactylus xanti, Sceloporus orcutti, Urosaurus nigricaudus* (*sensu* Grismer 1994), *Crotalus mitchellii, Elaphe rosaliae, Eridiphas slevini,* and *Lichanura trivirgata.* Of these, *Coleonyx switaki, Lichanura trivirgata,* and *Crotalus mitchellii* are reported as being present by ranchers at Rancho San Ramón in the Sierra Santa Clara but this could not be confirmed by us. The same ranchers say that *Crotaphytus vestigium, Petrosaurus thalassinus,* and *Elaphe rosaliae* are absent from the Sierra Santa Clara. Additional species reported as being present from

Fig. 22. Typical *Xantusia vigilis* habitat from within the Sierra Santa Clara.

the Sierra Santa Clara but not confirmed by us are *Leptotyphlops humilis, Chilomeniscus cinctus, Masticophis flagellum, Lampropeltis getula,* and *Pituophis melanoleucus.* We would be surprised if these latter taxa did not occur throughout the Vizcaíno Peninsula owing to the wide range of habitats they occupy elsewhere in Baja California and the fact that they are known from other Vizcaíno Desert localities further east (Grismer 1994). We also suspect that *Arizona elegans pacata* and *Scaphiopus couchii* occur in this region as well, although they were not reported as being present by the ranchers. *Arizona e. pacata* ranges widely both north and south of the Vizcaíno Peninsula along the Pacific coastal desert of Baja California (Dixon and Fleet 1976; Reynoso 1990), and *S. couchii* is known from sandy habitats throughout central Baja California (Wasserman 1970).

We were very surprised at the apparent absence of *Xantusia vigilis* from the low-lying areas within the Sierra Santa Clara. This area supports a dense and extensive stand of *Yucca valida* (Fig. 22), a vegetational component with which this species is known to occur (Bezy 1982), but we were unable to find any specimens. We did note an unusally high density of the bark scorpion *Centruroides exilicauda* within the preferred microhabitat of *X. vigilis* and perhaps this scorpion is competitively excluding *X. vigilis.*

Also absent from the arroyos within the Sierra Santa Clara, as well as the Sierra Vizcaíno, was *Callisaurus draconoides crinitus.* This subspecies is highly adapted to living on the extremely fine aeolian sand of the Vizcaíno Desert (Norris 1958) and is widely distributed around the perimeter of these mountains. The substrate of the arroyo bottoms within these ranges is apparently too rocky and may prevent this habitat specialist from entering. However, such areas do increase the diversity

of reptiles within the boundaries of these ranges by serving as dispersal corridors for other lowland species such as *Gambelia wislizenii copei, Dipsosaurus dorsalis dorsalis, Phrynosoma coronatum* (*sensu* Grismer and Mellink 1994), *Sceloporus magister monserratensis,* and *Cnemidophorus hyperythrus hyperythrus* that would not normally occur in extremely rocky mountain areas.

Resumen

Una inspección herpetofaunal de la Península de Vizcaíno de Baja California Sur reveló muchas localidades nuevas por la herpetofauna de Baja California. Algunas de estas especies son más parecidas a conespecíficas de Isla de Cedros de las de sus poblaciones respectivas peninsulares. La presencia de la especie mesófila relicta *Hyla regilla,* en la Sierra de Vizcaíno, sugiere que este region era mucho más mésico en el pasado. La existencia de taxa saxícola en la Península de Vizcaíno, sugiere que estas formas colonizaron las sierras mientras existieron como Islas Pacíficas durante las últimas diezmil años porque estas especies no podrían despersar a través el arenoso Desierto de Vizcaíno que corrientemente está separandolas de sus equivalentes peninsulares.

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Appendix I

Voucher photograph catologue numbers of the Los Ángeles County Museum of Natural History (LACM PC) for representatives of the newly reported taxa from the continental portion of the Vizcaíno Peninsula. The locations of study sites 1–5 are listed in the text.

FROGS: *Bufo punctatus,* sites 1 and 4 LACM PC 1233 and 1234 respectively. *Hyla regilla,* site 4 LACM PC 1235. LIZARDS: *Gambelia wislizenii copei,* sites 2 and 5 LACM PC 1240 and 1241

respectively. *Dipsosaurus dorsalis,* site 1 LACM PC 1239. *Sauromalus australis,* sites 1, 2, and 5 LACM PC 1243, 1244, and 1242 respectively. *Coleonyx variegatus abbotti,* sites 2 and 5 LACM PC 1237 and 1238 respectively. SNAKES: *Hypsiglena torquata,* site 1 LACM PC 1246. *Salvadora hexalepis klauberi,* site 1 LACM PC 1249. *Trimorphodon biscutatus* site 1 LACM PC 1250. *Crotalus enyo,* sites 2 and 4 LACM PC 1251 and 1252 respectively. *Crotalus exsul,* sites 1 and 5 LACM PC 1254 and 1253 respectively.

Appendix II

Specimens Examined

The following is a list of the preserved material examined. Museum acronyms CAS = California Academy of Sciences, MVZ = Museum of Vertebrate Zoology and SDSNH = San Diego Natural History Museum.

Bufo punctatus.—BAJA CALIFORNIA: San Borjas SDSNH 17774; Cataviña SDSNH 19055–63, 40471, 41400–03, 41411, 43056–70; Arroyo Calamajué SDSNH 19911–12; 7 km N of San Javier SDSNH 45573–637; Bahía de San Luis Gonzaga SDSNH 47354, 47787; Agua Dulce SDSNH 47356–68; Cañón Providencia SDSNH 58648, 62854–60; Cañón Esperanza SDSNH 62897; Arroyo Cardonal SDSNH 62230–31. BAJA CALIFORNIA SUR: San José del Cabo SDSNH 39349–51; Loreto SDSNH 30352–56; El Arco mine SDSNH 30357; Rancho La Burrera SDSNH 45016–31, 57743–44; San Ignacio SDSNH 46022–30, 61312; La Laguna SDSNH 46054; Sierra Santa Lucía, San Sebastian SDSNH 46105–116, 46131; La Soledad SDSNH 46117–45; Todos Santos SDSNH 46809–23; near El Triunfo SDSNH 46832, 57745; Las Parras SDSNH 47355, 47788–91; Arroyo San Dionicio near Rancho Castro SDSNH 61320.

Hyla regilla.—BAJA CALIFORNIA: Isla de Cedros SDSNH 5267–71, 15972–76, 24358–66, 27623–44, 44460, 52973; Misión San Borja SDSNH 54166–75. BAJA CALIFORNIA SUR: San Ignacio CAS 90343–51, 90912–27, 136737, 136684–710; Boca de La Sierra CAS 91462, 123706–13.

Gambelia wislizenii.—BAJA CALIFORNIA: San José SDSNH 4071, 5078–80, 26752–53; 3 mi. E of Socorro SDSNH 4143; Isla de Cedros, south end SDSNH 5264, 15969; Isla de Cedros SDSNH 7249, 17411, 24340–42; 12 mi. E of El Arco SDSNH 17470; San Francisquito Bay SDSNH 18118; Valle de Trinidad SDSNH 18945–46; 40 mi. W of Los Ángeles Bay SDSNH 19787; Isla Cedros, canyon N of middle of island SDSNH 27693–95; 7 mi. NW San José SDSNH 36454; Rosario SDSNH 41613; 2 mi. San Simón SDSNH 42622; 8 mi. E El Rosario SDSNH 43007; NE of Mesa San Carlos SDSNH 45916.

Dipsosaurus dorsalis.—BAJA CALIFORNIA: 66.4 mi S of Mexicali SDSNH 46416–17; 8.3 km S on Laguna Salada rd. SDSNH 56448; Misión Santa Gertrudis SDSNH 17524–27; Bahía de los Ángeles SDSNH 18075–78, 19861, 37378–82, 52952; Valle Amarga SDSNH 18079; 1 mi NW of San Felipe SDSNH 37777; 15 mi. N of San Felipe SDSNH 18892, 18977; 30 mi. N of San Felipe SDSNH 38116; 3 mi. S of San Felipe SDSNH 18893, 38117, 38139; 17.5 mi. S San Felipe 18971; 16 mi. S San Felipe, Punta Diggs SDSNH 19873–74, 18976, 37772–76; San Matías Pass SDSNH 18975; between Puertocitos and Bahía de San Luis Gonzaga SDSNH 19857–59; 3.7 mi. N of Bahía de San Luis Gonzaga; 6–6.5 mi W of Bahía de los Ángeles SDSNH 41609–10; 12 mi. W of Bahía de los Ángeles SDSNH 19860, 41608; 10 mi. W of Bahía de los Ángeles SDSNH 41611; 7 mi. W of Misión San Borja SDSNH 19862; between 5 and 25 mi. N of Bahía de San Luis Gonzaga SDSNH 19868–82; 37 mi. N of Bahía de San Luis Gonzaga SDSNH 19883. BAJA CALIFORNIA SUR: 40 km S of El Arco SDSNH 30287–88; 16 km. E of El Arco SDSNH 7467–69; San Ignacio SDSNH 3862–64, 46035; 15 mi. S of Canipole SDSNH 30280; 3 mi. S of Canipole SDSNH 30281; 12 mi. S of Canipole SDSNH 30282–84; 43 mi. N of Canipole SDSNH 30285–86; 5 mi. inland from Mulegé SDSNH 52979; 27 mi. S of Santa Rosalía SDSNH 52980; 43 mi. S of Santa Rosalía SDSNH 53000; Rancho El Coyote (Bahía Concepción) SDSNH 53055-56; Cabo San Lucas SDSNH 2730–31, 10773–74, 17676–77, 30268; 13 mi. E of Cabo San Lucas SDSNH 39269–72; San José del Cabo SDSNH 17678–82; 6 mi S of Miraflores SDSNH 30273; 1 mi. W of Buena Vista SDSNH 30274; La Paz SDSNH 30275, 44119; 23 mi. W of La Paz SDSNH 30276; 0.7 mi E of San Antonio SDSNH 52974–76; La Laguna SDSNH 46053; La Burrera SDSNH 46377.

Sauromalus australis.—BAJA CALIFORNIA: Bahía de los Ángeles CAS 144062, 154922–24, MVZ 161279–82. BAJA CALIFORNIA SUR: San José de Comondú SDSNH 17707; La Paz SDSDNH 17708; Loreto SDSNH 30168; 33 mi. N of Canipole SDSNH 30169; 4.5 mi. N of Mulegé SDSNH 46459, 46465; 7.3 mi. N of Canipole SDSNH 46460; 4.0 mi. S of La Paz SDSNH 46461–63, 46466–67; 11.1 mi. S of Mulegé SDSNH 46468; 3.5 mi. S of Rancho Coyote SDSNH 53014; 9.6 mi. W.

Loreto SDSNH 53015-17; Bahía Agua Verde CAS 53710; 12.5 mi. SE of La Paz CAS 90582; 12.9 mi. E of La Paz CAS 91368; 9.9 mi. N of Loreto CAS 127460; 7 mi. SE of La Paz CAS 132569; 7 mi. S of La Paz CAS 134497; 6 mi. S of La Paz CAS 143158; 2.8 mi. N of Mulegé CAS 143697; 20 mi. N of Loreto CAS 143846–47; Santa Agueda CAS 146694, MVZ 161270–71; San Pedro de la Presa CAS 147719; Bahía Trinidad MVZ 96731; 2.4 mi. W of El Arco MVZ 161263.

Cnemidophorus hyperythrus hyperythrus.—BAJA CALIFORNIA: 1.6 km SE of Rancho Mezquital CAS 90504–05. BAJA CALIFORNIA SUR: 30 km N of Punta Abreojos CAS 147767–70.

Cnemidophorus labialis.—BAJA CALIFORNIA: 6 km E of Jesús María CAS 143163.

Cnemidophorus tigris.—BAJA CALIFORNIA: Misión San Borja SDSNH 17683–84, 19784; El Barríl SDSNH 18130; 2 mi. S of San Telmo SDSNH 18147; 7 mi. N of Punta Prieta SDSNH 18739; Valle de Trinidad SDSNH 18980-83, 20037; 12–15 mi. W of Bahía de los Ángeles SDSNH 19089, 19777–79; Bahía de los Ángeles SDSNH 19774–76, 19780–81, 38334; 42.5 mi. NW of Rosarito SDSNH 19785; 11 mi. N of Bahía de San Luis Gonzaga SDSNH 19786; Laguna Hansen SDSNH 20305; Ojos Negros SDSNH 23501; 5 mi. N of Lake San Faustino SDSNH 23502; Guadalupe Creek SDSNH 23738–39; Cañón de Burro SDSNH 25939; Bahía San Francsiquito SDSNH 30260–61; El Arco Mine SDSNH 30262; 40 mi. N of Punta Prieta SDSNH 30263; El Marmol SDSNH 30264, 41459–60; Rancho San Juan de Díos SDSNH 30265; 15 mi. N of Sangre de Cristo SDSNH 30266–76; 20 mi. W of El Marmol SDSNH 37422; 5 mi. W of Tecate SDSNH 38136–38; 2 mi. N of San Simón SDSNH 42620–21; 14 mi. E of El Rosarito SDSNH 43006; Round Top Mountain Bahía de los Ángeles SDSNH 30420–21. BAJA CALIFORNIA SUR: Bahía Tortuga SDSNH 3935–36; 2 mi N Queretaro SDSNH 30252–54; Loreto SDSNH 253–54; Rancho Santa Rita del Coyote SDSNH 46078; Bahía Concepción 50638–39; Punta Pulpito SDSNH 50640; 5.9 mi W of San Ignacio SDSNH 53018; 1.5 mi S of Rancho Coyote SDSNH 53019; 7.9 mi W Misión San Javier SDSNH 53020; 25 mi S El Arco SDSNH 30259; 17 mi NE Insurgentes SDSNH 46867–68, 57739–40.

Trimorphodon biscutatus.—BAJA CALIFORNIA: 1.5 mi. W of El Metate SDSNH 1363; El Pedregoso SDSNH 1679; on N side of rd. to Bahía de Los Ángeles (km. 52) SDSNH 2554; near San Vicente SDSNH 49386; 3 mi. E of Alaska SDSNH 38048; 11 mi. S of El Rosario SDSNH 46804. BAJA CALIFORNIA SUR: 8 mi. S of Puerto Escondido SDSNH 1029; 2 mi. E of San Ignacio SDSNH 1367, 1713; San Ignacio SDSNH 1688, 3818; 17.5 km. N of Cabo San Lucas SDSNH 1771; 68.5 km N of Cabo San Lucas SDSNH 1772; 6 km S of La Paz SDSNH 1773; 1 km S of El Triunfo SDSNH 1774; Rancho El Salto (S of La Paz) SDSNH 1845; 17 km S of La Paz SDSNH 1846; Ancón SDSNH 2163, 2366, 2300; 88 km N of Cabo San Lucas (Hwy 1) SDSNH 2260; San Antonio de la Sierra SDSNH 2353; 13 km S of Mulegé SDSNH 2745; Cabo San Lucas SDSNH 20507, 20165, 30362; Isla Cerralvo SDSNH 44395; La Burrera or La Laguna SDSNH 45209–12; 2.5 mi. S of San Antonio SDSNH 46836; 9 mi. N of El Triunfo SDSNH 46837; San Bartolo SDSNH 60306; 5 mi. S of San Antonio on Hwy. 1 SDSNH 61334. CALIFORNIA: Imperial and San Diego Counties SDSNH 105, 711, 846, 1062, 1364–66, 1526, 1529, 4423, 10020, 10301, 11750, 15501, 17054, 26733, 26819, 27136, 28330, 28562, 31235–36, 31442, 32848, 32937, 32947, 33234, 33326, 36353, 37342–43, 37869, 37924, 37997, 38048, 38980, 39223, 39256, 39455–56, 40152, 42070, 42091, 42678, 42768, 42798, 42847, 43317–18, 43274, 49386, 59197, 60207, 60230–31, 60303–04, 62279, 62573, 62714.

Crotalus exsul.—BAJA CALIFORNIA: Garcia SDSNH 2264; Bahía Santa Teresa SDSNH 3001; San José SDSNH 4806, 6079–80, 8848–49; 5 mi. S of Tijuana SDSNH 5015; 4 mi. E of Socorro Mine SDSNH 5134; San Quintín SDSNH 16709; 7 mi. E of El Rosario SDSNH 16710; near Aquajito Spring, Valle Trinidad SDSNH 16859; between Arroyo Las Cruces and Punta Cabras SDSNH 19690; Punta Banda SDSNH 19691; 25 mi. W. of Bahía de los Ángeles SDSNH 19716. BAJA CALIFORNIA SUR: Bahía Coyote SDSNH 2999; San Bruno SDSNH 3004; Loreto SDSNH 30389-92; Bahía Tortugas CAS 19826, 55886–87. Isla de Cedros CAS 135513, 135536, 56271–75, 59566–67, 59788, SDSNH 3008, 3495, 5199, 17340–41, 27727, 32564, 52919.

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Research Notes

Occurrence of the Anostracan *Branchinecta lindahli* (Packard) on the California Channel Islands

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The fairy shrimp, *Branchinecta lindahli,* occurs throughout the Great Plains, west of the Rocky Mountains, Baja California, Mexico, and on Guadalupe Island (Eng et al. 1990). This species is widely distributed throughout California, often occuring in temporary pools following winter and spring rains. In their authoritative work on California Anostraca, Eng et al. (1990) reported collections of *B. lindahli* from 66 sites throughout the southern half of the state. This species has been collected from the Mojave Desert, along the Central and South Coast mountains from San Luis Obispo to San Diego Counties, and in the southern half of the Central Valley. *B. lindahli* is the only anostracan occurring on the California Channel Islands and this species has previously been reported only from Santa Cruz Island (Eng et al. 1990). The occurrence of *B. lindahli* on Guadalupe Island west of central Baja California, Mexico (Belk and Lindberg 1979), and on Santa Cruz Island indicates *B. lindahli* may occur on other islands in the Channel Islands group. This paper documents the occurrence of this species on San Miguel, Santa Rosa, and San Nicolas Islands.

Branchinecta lindahli was initially collected from Santa Rosa Island in a seasonally astatic pool (defined in Eng et al. 1990) on 6 April 1991, in Pocket Field near the island's northwest end (lat 33°59′33″N, long 120°13′09″W). This species was collected from a similar habitat near Skunk Point at the east end of the island (lat 33°57′22″N, long 119°58′31″W) on 16 January 1992. Anostracans were collected from San Miguel Island on 24 February 1992, from a pool southeast of Green Mountain (lat 34°02′03″N, long 120°22′37″W). Pool habitats on Santa Rosa and San Miguel Islands were turbid, small (ca. 10 to 100 m^2), shallow ($\leq$1.0 m deep), swales occurring in arid grasslands. A population of *B. lindahli* was found in association with extremely high densities of *Daphnia magna* on San Nicolas Island in a perennially astatic pool ca. 0.6 km southwest of the northwest end of the airport runway (lat 33°14′40″N, long 119°28′23″W) on 10 March and 9 April 1992. This pool was similarly small (20–30 m^2) but relatively deep (>1.0 m). *B. lindahli* was also collected from a small (30–50 m^2), shallow, turbid pool on an old road along the northern terrace of the island (lat 33°15′35″N, long 119°28′40″W) on 8 April 1992.

The Santa Barbara Museum of Natural History (SBMNH) invertebrate collection contains *B. lindahli* specimens collected at the same location on San Miguel Island on 26 February 1980 and 21 March 1986 by D. Sweetnam and B. W. Arnold, respectively. Similarly, SBMNH specimens indicate this species was pre-

viously collected from San Nicolas Island on 14 February 1983 by T. Pearce and B. Roth and 19 October 1986 by D. R. Lindberg. Pearce and Roth collected from a different location than either location noted in this report. Lindberg's specimens were quite probably collected from the same pool southwest of the northwest end of the airport runway. In addition, specimens from Santa Cruz Island in the SBMNH collection were collected by F. G. Hochberg on 3 April 1982 from a temporary pond near Frazer Point. No evidence for previous collection of *B. lindahli* from Santa Rosa Island currently exists.

Voucher specimens (SBMNH 140145–140149) collected during this survey were deposited in the Department of Invertebrate Zoology, SBMNH. They are accompanied by species identifications verified by noted anostracan authority Denton Belk. Permission to collect was granted by the National Park Service and the United States Department of the Navy.

I wish to extend my thanks to B. Halvorson of the National Park Service and T. Keaney of the United States Department of Defense for permission to collect aquatic invertebrates on these islands. Thanks to M. Conway, D. Richards, and M. Senning for field assistance. E. Hochberg graciously provided previously collected specimens for examination and also granted the use of SBMNH equipment and facilities. Thanks to Denton Belk for expert verification of specimen identification. The generous assistance of J. Dugan, C. Eriksen, and D. Hubbard in reviewing this manuscript was greatly appreciated.

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Middle Miocene Pholadid Borings at the Base of the Isidro Formation, Arroyo Mezquital, Baja California Sur, Mexico

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Abstract.—Abundant sediment-infilled clavate (club-shaped) borings, assignable to ichnogenus *Gastrochaenolites,* are reported from the base of the Miocene Isidro Formation, Baja California Sur, Mexico. The infilled borings were made by pholadid bivalves that lived in a nearshore-marine environment on a semi-consolidated substrate ("*Glossifungites*" ichnofacies). Some borings are connected by horizontal burrows that are sculptured (*Spongeliomorpha*) or unsculptured (*Thalassinoides*). The localized pholadid community was short lived and abruptly terminated by an influx of sediment.

During the course of field investigations in Baja California Sur, Mexico, an assemblage of ichnofossils was found in the Isidro Formation at California State University, Northridge (CSUN) locality 1495 near the mouth of Arroyo Mezquital about 13.5 km south of the village of San Juanico on the Pacific coast (Fig. 1). The assemblage is at the erosional contact between the Eocene Bateque Formation and the overlying Miocene Isidro Formation. The ichnofossils are dominated by sediment-infilled clavate (club-shaped) borings that range in length from 5 to nearly 30 cm. The contact that contains these infilled borings is well exposed, at a height of some 40 m on the side of a mesa that borders the southeast margin of the arroyo. The infilled borings are confined to an approximate linear distance of 1 km along the mesa wall, which is deeply incised by a number of semi-circular re-entrants.

Fischer (1990), in a general review of the subject of boring bivalves, showed pictures of infilled borings from the Isidro Formation as examples of cylindrical-shaped burrows, but he did not give any locality data nor any ichnological details.

The purposes of this paper are to describe the ichnofossils and to consider their paleoenvironment. Abbreviations used are: CSUN, California State University, Northridge: LACMIP, Natural History Museum of Los Angeles County, Los Angeles, Invertebrate Paleontology Section.

Geologic Setting

The uppermost 30 m of the Bateque Formation at Arroyo Mezquital is a vertical exposure of bioturbated, yellow, very fine-grained sandstone that is moderately indurated. Rare lamination is preserved and it seems to be parallel or nearly so. Scattered shell fragments are present as are some oblique *Ophiomorpha*-like bur-

Fig. 1. Index map showing location of the study area and CSUN loc. 1495.

rows filled with the same type of sediment found in the Bateque Formation country rock. Squires and Demetrion (1992) interpreted the paleoenvironment of the Bateque Formation in this area to be "middle shelf" and equivalent to a depth range between normal-storm wave base and maximum-storm wave base. Microfossil evidence indicates a middle Eocene age equivalent to the Pacific coast molluscan "Tejon Stage." For a more complete discussion of the Bateque Formation at this locality, see Squires and Demetrion (1992).

Approximately 15 m of the overlying Isidro Formation is exposed in near-vertical to vertical cliffs. The outcrop consists of several horizontal shell-hash layers (coquinas), ranging in thickness from 10 cm to 2 m, in a white, coarse-grained sand matrix, separated by grayish-green mudstone and sandstone that are virtually barren of macrofossils. The shell-hash layers tend to be variable in terms of dominant genera. Barnacles and oysters, as well as pectinids and clypeasteroid echinoids (sand dollars), are the main components. Post-mortem transport of the fossils was minimal as some of the bivalves are articulated and delicate sculpture on the shells of most of the fossils has not been worn off. The stratigraphically lowermost layer is dominated by barnacles (as individuals up to 5 cm height, and

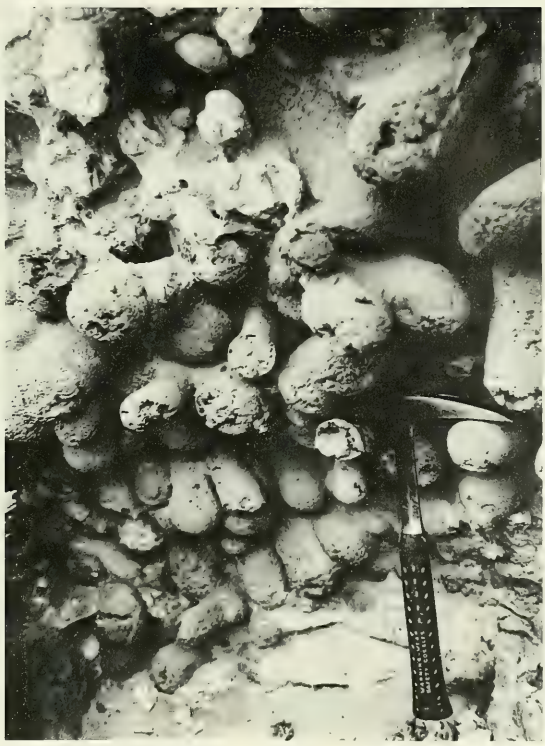

Fig. 2. Infilled clavate borings along basal contact of the Isidro Formation at CSUN loc. 1495 (where a large block of rock has fallen from the cliff face). Hammer is 30 cm in length.

in clusters) with significant numbers of small-sized (up to 3 cm height) and large-sized (up to 8 cm height) pectinids, internal molds of *Turritella* and unidentified bivalves, and rarer components of clypeasteroid echinoids, large-sized (up to 17 cm length) oysters, and bone fragments. A nearshore depositional environment is indicated by the fossil content and lack of significant post-mortem transport of the fossils. A late middle Miocene age for the Isidro Formation at this locality has been reported by Squires and Demetrion (1993) on the basis of the presence of the sand dollar *Astrodapsis bajasurensis* Squires and Demetrion, 1993.

The horizontal contact of the two formations at the study site is clearly delineated by a remarkable trace-fossil assemblage. The contact is accessible in two ways. A number of spurs have been created by erosion of prominences along the cliff face. They are rather steep and precarious. Safer, but more limited, access is possible at several places where huge blocks have fallen from the cliff face. Some of these fallen blocks provide excellent specimens of the trace fossils (Fig. 2). *In situ,* the contact presents a limited three-dimensional view due to differential weathering of less highly indurated Eocene substrate penetrated by Miocene borers.

Ichnofossils

Sediment-infilled clavate borings.—Infilled borings are predominantly smooth but rare individuals (Figs. 3A, B) display basal concentric, serrated tool marks

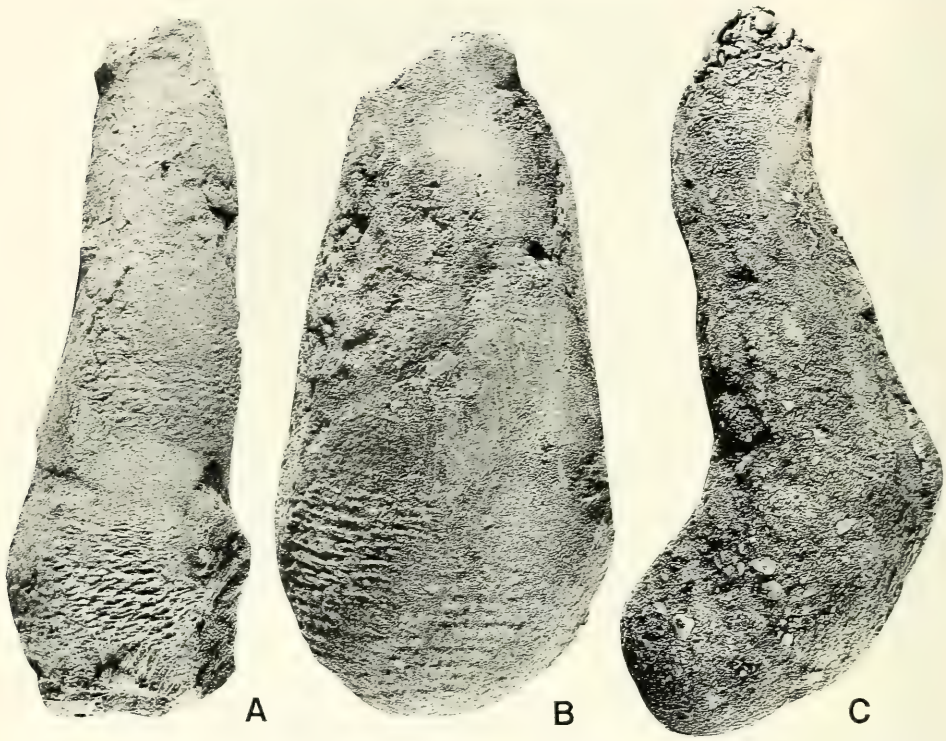

Fig. 3. Individual infilled, clavate borings of *Gastrochaenolites* from CSUN loc. 1495. (A–B), Rare specimens showing basal concentric, serrated tool marks accentuated by the presence of gypsum. A, Hypotype LACMIP 12271, 13 cm in length, ×1.4. B, Hypotype LACMIP 12272, 14.2 cm in length, ×1.5. C, Specimen showing prominent bend near base, hypotype LACMIP 12273, 16.5 cm in length, ×1.7.

that are accentuated by the presence of gypsum. Shape is elongate with little or no neck constriction. Cross section is circular throughout, and maximum diameter is close to the hemispherical base. Infilled borings are usually straight, but some (Fig. 3C) have a bend that ranges from 10 to 45 degrees from the vertical. Measurement of 25 individuals provide the following: length ranges from 4 to 27 cm, maximum diameter ranges from 1.3 to 9.5 cm, and conical angle ranges from 12 to 17 degrees. A number of infilled borings have a hemispherical or slightly pointed terminal protrusion of 1 to 2 cm in length. These small protrusions are probably secondary burrows that were begun and then abandoned.

Sediment infill is mostly coarse sandstone similar to the immediately overlying lithology. The fill sandstone can be poorly cemented to well-indurated, and there can be shell fragments and well-rounded volcanic pebbles (up to 13 mm in diameter). Clear-crystalline gypsum is also common. Sectioned infilled borings commonly display well-delineated secondary infilled borings or burrows.

In situ infilled borings commonly have the upper terminus cut by the overlying shell-hash layers, and only rarely do the borings extend a few centimeters upward into the overlying strata. Densities of infilled borings range from 1 to 2 per linear meter at the eastern and western margins of the study area to well in excess of

Fig. 4. Infilled clavate borings interspersed with horizontal burrows of *Thalassinoides* along *in situ* basal contact of the Isidro Formation at CSUN loc. 1495. Square end of hammer is 2 cm in width.

100 per square meter in the central part of the study area. With increasing density, there is a pronounced tendency for infilled borings to become longer with more bulbous ends, for the infilled borings to display directional changes, and for penetration angles of the infilled borings to deviate from vertical and become as much as 45 degrees from the vertical to nearly horizontal. Infilled borings do not intersect each other, even where they are crowded.

According to Kelly and Bromley (1984), the geologic range for clavate borings in lithic substrates is Jurassic to Recent. Miocene reports of infilled clavate borings are common, and examples that resemble those from the Isidro Formation have been reported from Japan (Uozumi and Fujie 1956), California (Adegoke 1966), the Gulf of Mexico (Warme and McHuron 1978), Poland (Radwanski 1977) and New Zealand (Bradshaw 1980). Modern borings that resemble those from the Isidro Formation have been reported from Oregon by Evans (1970), from San Diego by Warme (1970), and from the Texas Gulf Coast by McHuron (1976). The resemblance involves size and shape, substrate affected, presumed environment of creation, and associated trace fossils. Based on these similarities, the infilled clavate borings at CSUN loc. 1495 are identified as *Gastrochaenolites*. Kelly and Bromley (1984) provided a detailed review of this ichnogenus.

Horizontal burrows.—Approximately five percent of the infilled clavate borings are connected by horizontal burrows (Fig. 4) with circular cross sections whose diameters range from 1.5 to 2.5 cm. The fill in these burrows is similar to that in the infilled clavate borings. Most of these burrows have walls which exhibit extensive scratch marks, although a few bear no sculpture. In the cases where burrows branch, they usually do so at a 60-degree angle. Some burrows loop out from and then re-enter an individual infilled boring. The sculptured horizontal burrows are assigned to *Spongeliomorpha* on the basis of comparison to descriptions by Ekdale et al. (1984, pp. 31, 33, 192), and the unsculptured horizontal

burrows are assigned to *Thalassinoides* on the basis of comparison to illustrations in Ekdale et al. (1984, figs. 3-5, 15-5).

Ichnofacies

According to Ekdale et al. (1984), firm but uncemented substrates are associated with the ichnofacies *Glossifungites,* which is characterized by the ichnogenera *Gastrochaenolites, Spongeliomorpha,* and *Thalassinoides.* Pemberton and Frey (1985) asserted that the *Glossifungites* ichnofacies typically is associated with dewatered muds. They also noted that thalassinoidean traces in this ichnofacies commonly display well-developed cheliped sculptings. The *Trypanites* ichnofacies, as described by Ekdale et al. (1984), is associated with fully lithified substrates (generally a relict surface) and can also contain the ichnogenus *Gastrochaenolites.* Recognizing that the two ichnofacies are intergradational, we assign the trace-fossil assemblage at the base of the Isidro Formation to the *Glossifungites* ichnofacies on the basis of the ichnogenera present and the lack of complete cementation of the Eocene substrate.

Discussion

On the basis of their strong resemblance to the morphology of modern borings described by McHuron (1976), Evans (1970), and Warme (1970), as well as to fossil borings whose producers have been positively identified (see references on Miocene borers in "Sediment-infilled clavate borings" section), we believe that the organisms responsible for the Isidro Formation borings were pholadid bivalves. Several other lines of evidence support this conclusion.

According to Pemberton and Frey (1985), pholadids dominate foreshore-like, wave-influenced deposits. Evans (1968a) noted that morphology of pholadid borings in a given substrate is controlled by population density, with greater crowding producing greater variability. McHuron (1976) observed that the same species of pholadids could produce borings with or without bioglyphic ornamentation (i.e., serrated tool marks), depending on the substrate hardness (harder substrates tend to diminish sculpture). Kennedy (1974) pointed out that pholadid borings in an open-coast marine environment tend to be filled with coarser sediments and that some secondary nestlers extract calcium carbonate from pholadid shells, thereby dissolving them. He also distinguished pholadid from mytilid borings on the basis of the virtually constant cross-sectional area of mytilid borings and the fact that they are bilaterally symmetrical, in contrast with the conical body and circular cross sections of pholadid borings.

Given the evidence at hand and the assumption that pholadid bivalves produced the clavate borings, it is possible to interpret the environmental conditions at the base of the Isidro Formation. Incompletely cemented Eocene deposits of the Bateque Formation were subaerially exposed and eroded. Subsequent transgression by the Miocene seas provided a relatively hard surface which was colonized by pholadid borers. Ekdale et al. (1984) stated that heavy infestation of lithic substrates by ichnogenus *Gastrochaenolites* is large a shallow-water phenomenon. A shallow-water environment for the Isidro Formation borers is also indicated by the shell-hash infill of the boreholes. The shell-hash contains remains of nearshore animals that do not show evidence of significant post-mortem transport. As pholadid colonization progressed, secondary inhabitants took advantage of

the pioneering efforts of the pholadids and became nestlers in the borings. At this point, a departure from "textbook" descriptions takes place.

According to Warme and McHuron (1978), the species richness of modern-marine hardgrounds is due to borers that open the substrate "frontier" for secondary settlers. They stated that abandoned borings become inhabited and modified by an assortment of organisms. Warme (1970) noted that in advanced stages, borings become interconnected to form networks of passageways. Kennedy (1974) remarked that erosion rates are higher where pholadids colonize, due to a weakened substrate and wave action. Evans (1968b) found that erosion in such areas increased by a factor of 24. However, in the assemblage studied at Arroyo Mezquital, there is no ichnologic evidence of species richness. Nor is there evidence of significant erosion of the substrate, even in the populous central area of study.

Our interpretation is that the set of environmental conditions that gave rise to the pholadid community was very short-lived. The central, "seed" area of the colony reached a population maximum and the secondary settling by horizontal-burrowing crustacean opportunists then began while the pholadids were in the process of peripheral expansion. Abruptly, a sediment influx overwhelmed the filter-feeding pholadids. The few borings that extend upward into the overlying strata represent the efforts of surviving crustaceans. Ultimately, in a regimen of increasing storm-generated sedimentation, they too perished.

Acknowledgments

We thank George L. Kennedy (San Diego, California) for sharing his knowledge about pholadid borings. The manuscript benefitted from the reviews of two anonymous referees.

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